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Bulletin of the British Museum (Natural History)

The Thelypteridaceae of Ceylon

W. A. Sledge

Botany series Vol 8 No 1 26 February 1981

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The Thelypteridaceae of Ceylon

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Synopsis

Thirty-four species of thelypteroid ferns from Ceylon (Sri Lanka) are described and discussed, and keys are provided. *Amauropelta hakgalensis* Holttum, *Trigonospora angustifrons* Sledge, *T. glandulosa* Sledge and *T. obtusiloba* Sledge are newly described, as are *Christella papilio* var. *repens* Sledge and *Metathelypteris flaccida* var. *repens* Sledge. Four new combinations are made: *Trigonospora caudipinna* (Ching) Sledge, *T. zeylanica* (Ching) Sledge, *Stegnogramma pozoi* var. *mollisssima* (Kunze) Sledge, and var. *petiolata* (Ching) Sledge. *Thelypteris confluens* (Thunb.) Morton is newly reported from Ceylon. Evidence for the occurrence of *Christella meeboldii* (Rosenst.) Holttum and *C. subpubescens* (Blume) Holttum and for the status of the former species is presented.

Introduction

The ferns described in this paper were not recognised as a separate group of species by nineteenth-century botanists. Classifications then adopted attached overriding importance to soral characters, and the similarities of these characters in thelypteroid and dryopteroid ferns led to species from both groups being included in the same genus. In Beddome's *Handbook to the Ferns of British India, Ceylon and the Malay Peninsula* (1883), nearly all the ferns described here were referred to *Lastrea* or *Nephrodium*, according to whether the species were free-veined or had anastomosing veins. A separation based on venation was still being employed 70 years later with *Lastrea*—or *Thelypteris*—and *Cyclosorus* as the currently used generic names, though the artificial nature of the separation was being increasingly recognised.

Christensen (1911) was the first to draw attention to the characters which distinguish thelypteroid from dryopteroid ferns, though it was not until almost 30 years later that family rank was assigned by Ching (1940) to the Thelypteridaceae. Cytological information has since supplied strong evidence in support of the morphological and anatomical grounds for the separation. Within the Thelypteridaceae the range of chromosome numbers is 27–36 (excluding 33), whereas *Dryopteris* and its allies are based on 41. The characters which distinguish thelypteroid ferns are: the possession of rhizome scales bearing acicular hairs on their margins and, usually, on their surfaces; stipes always containing two vascular bundles at the base uniting upwards to give a single deeply concave strand; acicular hairs invariably present on both the upper surface of the main axis and the pinnae; sinuses between the pinna lobes normally closed at the base by a translucent membrane.

Though the family Thelypteridaceae has been generally accepted by pteridologists, no general agreement exists as to its subdivision. Ching (1963) described 18 genera from mainland Asia; Holttum (1971) recognised 23 genera in the Old World, whilst Pichi-Sermolli (1977) listed 32 genera for the world as a whole. However, generic boundaries, as defined in these schemes, are too finely drawn—as in the Hymenophyllaceae—to be acceptable to some botanists. Moreover Wood's (1973) observations have shown that correlation between gross morphology and spore morphology is often lacking, especially amongst those species groups having n = 36 as a base chromosome number. Morton (1963) included all species within a single genus *Thelypteris*. Iwatsuki (1964) and Smith (1971, 1973, 1974), who have made special studies of Asiatic and New World species respectively, take a similarly conservative view, referring most species to *Thelypteris*, within which most

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of the genera of Ching and Holttum are treated as sections or subgenera. Such differences of treatment are largely a matter of subjective judgements, but since both the morphological and cytological diversity within the family seem to me to be too great to warrant the inclusion of all species within a single genus, I have followed Holttum's classification.

About half of the species described here were recognised by Thwaites, Beddome and their contemporaries, though often under different specific epithets. Some names used by them covered more than one species, notably so in the case of *Nephrodium molle* and *Lastrea calcarata.* Both these names, as employed by Beddome and Thwaites, included several different species. The former collective species incorporating *Christella parasitica* and related taxa, was shown by Manton & Sledge (1954) to produce hybrids in nature in Ceylon* (Sri Lanka). Subsequent experimental work (Panigrahi & Manton (1958), Ghatak & Manton (1971)) produced several hybrid combinations, and the variability and consequent difficulty in naming some wild gatherings is doubtless connected in some way with hybridisation. Experimental studies with the other collective species have not been made, but the polymorphism of the *Trigonospora calcarata* aggregate in Ceylon and south India, where it has long been a source of taxonomic confusion, may well also be due, at least in part, to hybridisation between the several taxa which the name embraces. In the following account I recognise seven species of *Christella* and seven species, three of them newly described, of *Trigonospora,* but further observations in the field and more cytotaxonomic studies are required, especially in *Trigonospora,* before a full understanding can be reached. Apart from these genera, one new species is described and two species are recorded for the first time from Ceylon.

The thelypteroid ferns of Ceylon are mostly plants of medium to high elevations growing terrestrially in shady forest, partially shaded banks, in moist ground near streams, or in open swamps. A few are exclusively low altitude ferns. These include *Ampelopteris prolifera, Cyclosorus interruptus, Trigonospora glandulosa,* and *T. zeylanica,* all of which grow in marshes or by the sides of streams. Some species, such as *Amphineuron opulentum, A. terminans, Christella parasitica, Macrothelypteris torresiana, Pneumatopteris truncata, Pronephrium triphyllum, Trigonospora calcarata,* and *T. obtusiloba,* grow both in the low country and in the hills, some of them ascending to 1250 m or more. Another group is confined to the higher mountains of the interior, growing mostly between 1500–2200 m. This group includes *Amauropelta hakgalensis, Christella papilio, Metathelypteris flaccida, Parathelypteris beddomei, Pseudophegopteris pyrrhorhachis, Stegnogramma pozoi* var. *petiolata,* and *Trigonospora caudipinna.* Other species are mainly found at altitudes between 500–1500 m.

Some of the commonest ferns in the country belong to this family. The most widely distributed and abundant species are *Christella dentata, C. parasitica, Macrothelypteris torresiana, Sphaerostephanos arbuscula, S. unitus* and *Trigonospora obtusiloba.* Many other species, though more restricted in distribution by altitude or ecology, are abundant in suitable terrain over considerable areas. The following species are at present known from only a few or single localities: *Amauropelta hakgalensis, Ampelopteris prolifera, Christella meeboldii, C. subpubescens, C. zeylanica, Sphaerostephanos subtruncatus, Thelypteris confluens, Trigonospora angustifrons,* and *T. glandulosa.*

The geographical distribution of some species is wide. *Christella hispidula* and *Cyclosorus interruptus* are pan-tropical; *Ampelopteris prolifera, Amphineuron opulentum, Christella dentata, Macrothelypteris torresiana, Sphaerostephanos unitus,* and *Thelypteris confluens* spread from tropical or subtropical Africa eastwards across Asia to the Pacific; *Christella dentata* and *Macrothelypteris torresiana* also occur as adventives in tropical America. Most species are confined to south-east Asia ranging eastwards to varying extents, often to China and Japan or through Malesia, whilst *Amphineuron terminans* and *Pronephrium triphyllum* reach northern Queensland in Australia.

Of the species with a more restricted range, *Christella meeboldii, Pronephrium thwaitesii* and *Pseudocyclosorus tylodes* are known only from Ceylon and southern India. *Sphaero-*

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*The name Ceylon is used for Sri Lanka in order to conform with the author's account of the Dryopteroid ferns, which appeared in Volume **5** (1973).

stephanos subtruncatus occurs elsewhere in south-west India and the Seychelle Islands, and *S. arbuscula* in the Mascarene Islands and Madagascar (with a subspecies in east Africa). *Trigonospora calcarata* was described from Java and is reported also from Sumatra, whilst *Stenogramma pozoi* var. *petiolata* and *Christella zeylanica* are known to occur outside Ceylon only in Java and the Nicobar Islands respectively.

Six species are endemic to Ceylon: *Amauropelta hakgalensis, Pronephrium gardneri* (probably now extinct), *Trigonospora obtusiloba, T. angustifrons, T. glandulosa* and *T. zeylanica.*

In the citations of specimens under each species the C.P. (Coll. Peradeniya) numbered sheets distributed by Thwaites have been listed first, since sets of these are to be found in many herbaria and the numbers have been widely quoted. Thwaites rarely indicated, save in the most general terms, where his specimens had been collected. Much of his material was doubtless gathered and brought in by native collectors. The pencilled localities found on many of the sheets at Peradeniya indicate localities whence the species had been recorded, and not where the specimen on the sheet had been gathered. Since errors of identification occur, the localities are not always reliable.

Gardner also distributed numbered sheets of Ceylon plants, the ferns in his exsiccatum being included under the numbers 1053–1271. These are listed next in the specimen citations. Gardner's numbers are quoted in parentheses after the C.P. numbers in Thwaites' *Enumeratio Plantarum Zelaniae* (1864), whilst his own collection of Ceylon ferns, giving name, place of origin and date of collection on each sheet, is at Cambridge. Other gatherings by Gardner at Kew and elsewhere bear numbers only. The specimens of other collectors are arranged geographically, with unlocalised gatherings placed at the end.

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BM: British Museum (Natural History), London; CGE: Botany School, University of Cambridge; E: Royal Botanic Gardens, Edinburgh; K: Royal Botanic Gardens, Kew; L: Rijksherbarium, Leiden; P: Muséum National d'Histoire Naturelle, Paris; PDA: Botanic Gardens, Peradeniya; US: United States National Museum, Smithsonian Institution, Washington, U.S.A.; WRSL: Museum of Natural History, Wroclaw, Poland.

Abbreviations used in the citation of specimens are those adopted in the *Index Herbariorum* (Holmgren & Keuken, 1974).

Professor R. E. Holttum's unrivalled knowledge of thelypteroid ferns has been freely available to me whenever I sought his opinion and I thank him for his valuable comments and unfailing helpfulness. I am grateful to Mr J. W. Grimes for supplying scanning electron microscope photographs of spores, to Miss Antonia Lant for making the drawings, and to Mr G. A. Shaw for typing my manuscript.

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Taxonomy

Key

1	Veins free	2
–	Veins anastomosing	10
2(1)	Rhachis reddish-brown, fronds bipinnate or deeply bipinnatifid, sori exindusiate	**Pseudophegopteris pyrrhorhachis** (p. 5)
–	Rhachis not reddish-brown; sori round and indusiate, or elongate and exindusiate	3
3(2)	Fronds bipinnate, tripinnatifid	**Macrothelypteris torresiana** (p. 7)
–	Fronds pinnate or bipinnatifid	4
4(3)	Pinnae pinnatifid with lobed pinnules, veins forked, not reaching the margins	**Metathelypteris flaccida** (p. 8)
–	Pinnae lobed to pinnatifid with entire pinnules, veins simple, reaching the margins	5
5(4)	Sori elongate, exindusiate, pinnae shallowly lobed	**Stegnogramma pozoi** var. **petiolata** (p. 49)
–	Sori round, indusiate, pinnae pinnatifid	6
6(5)	Rhizome creeping	7
–	Rhizome erect	8
7(6)	Under surface of pinnae with scattered glands and hairy costae	**Parathelypteris beddomei** (p. 11)
–	Under surface of pinnae eglandular, costae bearing scales	**Thelypteris confluens** (p. 12)
8(6)	Lower pinnae not reduced or if so not abruptly	9
–	Lower pinnae abruptly reduced to tubercles on the stipe	**Pseudocyclosorus tylodes** (p. 25)
9(8)	Fronds decrescent, under surface of pinnae bearing hooked hairs, indusia minute	**Amauropelta hakgalensis** (p. 9)
–	Fronds not decrescent, under surface of pinnae without hooked hairs, indusia evident	**Trigonospora** (key on p. 15)
10(1)	Sori elongate, exindusiate	11
–	Sori round, indusiate	14
11(10)	Proliferating buds present on rhachis	**Ampelopteris prolifera** (p. 14)
–	Proliferating buds absent from rhachis	12
12(11)	Up to 9 pairs of pinnae, no hooked hairs on under surface of pinnae	**Stegnogramma pozoi** var. **petiolata** (p. 49)
–	One to four pairs of pinnae, lower surface of pinnae bearing hooked hairs	13
13(12)	Fronds with 1–2 pairs of pinnae, terminal pinna entire	**Pronephrium triphyllum** (p. 47)
–	Fronds with 2–4 pairs of pinnae, terminal pinna pinnate or pinnatifid	**Pronephrium thwaitesii** (p. 47)

14(10) At least 3 pairs of veins anastomosing 15
– 1–2 pairs of veins anastomosing 16
15(14) Margins of pinnae shallowly lobed, 3–5 pairs of veins anastomosing . **Pronephrium articulatum** (p. 45)
– Margins of pinnae crenate, 7 pairs of veins anastomosing . **Pronephrium gardneri** (p. 46)
16(14) Rhizome erect 17
– Rhizome creeping 20
17(16) Pinnae eglandular beneath 18
– Pinnae with yellow glands beneath 19
18(17) Pinnae glabrous beneath . . . . **Pneumatopteris truncata** (p. 42)
– Pinnae hairy beneath . . . . **Christella hispidula** (p. 33)
19(17) Lower pinnae progressively reduced . . **Sphaerostephanos arbuscula** (p.43)
– Lower pinnae abruptly reduced . . **Sphaerostephanos subtruncatus** (p. 44)
20(16) Lower pinnae abruptly reduced . . . . **Sphaerostephanos unitus** (p. 44)
– Lower pinnae not or gradually reduced 21
21(20) Lower pinnae not shortened 22
– Lower pinnae gradually decreasing in size . . . **Christella** (key on p. 29)
22(21) Costae glabrous or sparsely scaly beneath . . **Cyclosorus interruptus** (p. 13)
– Costae hairy and often glandular beneath 23
23(22) Lower pinnae narrowed at their bases, not deflexed 24
– Lower pinnae not narrowed at their bases, usually deflexed . **Christella parasitica** (p. 29)
24(23) Margins lobed ⅔ to costa, at most one pair of veins fusing, sometimes basal veins free . . . . **Amphineuron opulentum** (p. 27)
– Margins lobed ¼ to ½ to costa, 1½–2 pairs of veins fusing . **Amphineuron terminans** (p. 28)

I. PSEUDOPHEGOPTERIS Ching

in *Acta phytotax. sin.* **8** : 313 (1963). Holttum in *Blumea* **17** : 12 (1969).

Caudex erect or creeping; basal scales thin, brown, with scattered superficial hairs but lacking conspicuous marginal or apical hairs; stipe and rhachis glossy, usually red-brown in colour; fronds elongate, bipinnate with the lower pinnae ± reduced and more widely spaced; pinnae opposite or nearly so, the pinnules adnate and usually ± deeply lobed and often connected by a narrow wing; upper surface of costae not grooved; veins usually forked, not reaching the margins, tips ± thickened; unicellular acicular and/or capitate hairs and much reduced filiform scales present on lower surfaces of rhachis and pinna rhachis; sori exindusiate, round or slightly elongated, sporangia hairy or glabrous; spores usually with a slightly raised surface reticulum, lacking a winged perispore. n = 31.

Holttum has monographed the genus in *Blumea* **17** : 12–25 (1969). He recognises 20 species, mostly from south-east Asia, but with outlying species, often very restricted in distribution, ranging from St Helena eastwards to Hawaii and Samoa.

1. **Pseudophegopteris pyrrhorhachis** (Kunze) Ching

in *Acta phytotax. sin.* **8**: 315 (1963).—*Polypodium pyrrhorhachis* Kunze in *Linnaea* **24** : 257 (1851). Type: India, Nilgiris, *Weigle-Schaeffer 6* (?B, not seen).—*Lastrea pyrrhorhachis* (Kunze) Copel., *Gen. Fil.* : 139 (1947) p.p.—*Macrothelypteris pyrrhorhachis* (Kunze) Pic. Ser. in *Webbia* **24** : 716 (1970).

Polypodium distans D. Don, *Prod. Fl. Nepal.* : 2 (1825), non Kaulf. (1824). Baker in Hook. & Baker *Syn. Fil.* : 308 (1867) p.p. Type : Nepal, *Wallich* (not located).—*Phegopteris distans* (D. Don.) Mettenius in *Abh. senckenb. naturforsch. Ges.* **3** : 16 (1858). Bedd., *Handb. Ferns Brit. Ind.* : 292 (1883).

Nephrodium microstegium Hook., *Spec. Fil.* **4** : 119, t. 250 (1862). Type: Khasya, *J. D. Hook. & Thomson* (K).—*Lastrea microstegia* (Hook.) Bedd., *Ferns Brit. Ind.* : t.39 (1865).

Polypodium paludosum sensu Bedd., *Ferns South. Ind.* : t. 168 (1863), non Blume (1829).—*Thelypteris paludosa* sensu K. Iwats. in *Acta phytotax. geobot. Kyoto* **19** : 11 (1961). *Mem. Coll. Sci. Kyoto Univ.* B, **31** : 139 (1965) p.p.

Polypodium brunneum Wall., *Cat.* no. 333 (1829), *nom. nud.*—*Dryopteris brunnea* Christensen, *Index Fil.* : 255 (1905), *nom. nud.*—*Thelypteris brunnea* Ching in *Bull. Fan meml Inst. Biol.* (Bot.) **6**: 269 (1963), *nom. nud.*

Rhizome suberect or short-creeping, stipes 20–60 cm long, straw coloured below becoming suffused with red upwards and the *rhachis* always *reddish-brown in colour*; *lamina* 40–80 cm long, *bipinnate of deeply bipinnatifid* with about 20 pairs of free sessile *opposite pinnae,* the lower 2–3 pairs reduced and the lowermost pair more widely spaced on the rhachis; largest pinnae about 15 × 4 cm divided nearly or quite to the pinna-rhachis, the pinnules adjacent to the main rhachis pinnatifid half way to the costule, becoming progressively less incised then entire distally, *all with broad bases and contiguous or joined by a narrow wing on the axis of the pinna or quite free,* apex blunt or subacute, veins pinnate in the lobes, simple or forked, pellucid; upper surface short-hairy on costa and costules, lower surface with scattered, longer, spreading hairs on the costa and veins and about the margins of the lobes; texture herbaceous; *sori* small, *exindusiate,* mostly near the extremity of the basal acroscopic forks of the veins.

Collections: Thwaites C.P. 1288 (BM; CGE; K; P; PDA). Nuwara Eliya, moist open places, Oct. 1845, *Gardner* 1151 (CGE; BM; K). Adam's Peak, 1950 m, 14 Dec. 1950, *Sledge* 621 (BM). Nuwara Eilya, 10 May 1906, *Matthew* 637 (K). Same locality, *Freeman* 287, 288, 289, 290 (BM). Same locality, 21 Jan. 1908, *Bicknell* (P). Same locality, *Bradford* (CGE). Moon Plains, Nuwara Eliya, 1800 m, 23 Dec. 1950, *Sledge* 712 (BM). Adam's Peak, 14 Feb. 1908, *Matthew* (K). By track through jungle near Horton Plains, 2100 m, 19 Dec. 1950, *Sledge* 681 (BM). Forest above Le Vallon tea estate, 1350 m, 9 Feb. 1954, *Sledge* 1113 (BM). Blackwood Forest, Welimada-Haputala road, Badulla District, by stream, *c.* 1500 m, 18 Nov. 1976, *Faden* 76/345 (K). Unlocalised: *Walker* (K). *Robinson* 190 (K). *Wall* ex herb. *Hope* (P).

In marshy places and by stream banks at elevations of 1250–2100 m.

Southern India and Ceylon; northern India from Kashmir to Assam, west China, and Vietnam (Tonkin).

A frequent species at high elevations, growing in the open or in lightly shaded places. Readily recognised by its ruddy-coloured rhachis and opposite pinnae with the basal pinnules contiguous with or overlapping the frond axis.

Two cytotypes exist in Ceylon, a tetraploid and a hexaploid. The tetraploid, which appears to be the more frequent of the two, differs from the hexaploid in its somewhat narrower and more deeply lobed pinnules which, in the middle and distal pinnae, have more acute apices. Pinnae of the two types are illustrated in Manton & Sledge, *Phil. Trans. R. Soc.* B, **238** : 162, fig. 13 (1954).

II. MACROTHELYPTERIS (H. Itô) Ching

in *Acta phytotax sin.* **8** : 308 (1963).

Caudex short-creeping or erect; scales at base of stipe ± thickened at the base, with marginal and surface acicular or capitate hairs; fronds bipinnate—tripinnatifid with ± adnate pinnules, lowest pinnae not or little reduced; upper surfaces of costae not grooved; scales on rhachis narrow with thickened base and acicular hair-tip, hairs on lower surface of frond long, slender and multicellular; veins usually branched, not reaching margins; sori small, indusiate but indusium very small, sporangia usually bearing capitate hairs near annulus, spores with a ± winged perispore. $n = 31$.

Nine species: from Mascarene Islands throughout warmer parts of Asia eastwards from Japan to Australia (Queensland); Pacific Islands.

An account of the species has been given by Holttum in *Blumea* **17** : 25–32 (1969).

1. **Macrothelypteris torresiana** (Gaudich.) Ching

in *Acta phytotax. sin.* **8** : 310 (1963).—*Polystichum torresianum* Gaudich. in Freyc., *Voy. Bot.* : 333 (1828). Type: Mariana Island, *Gaudichaud* (P).—*Thelypteris torresiana* (Gaudich.) Alston, in *Lilloa* **30** : 111 (1960). K. Iwats. in *Mem. Coll. Sci. Kyoto Univ.* B, **31** : 151, 153 (1965).

Aspidium uliginosum Kunze in *Linnaea* **20** : 6 (1847). Type: cult. Hort. Bot. Leipzig, origin Java (formerly LZ, now destroyed).—*Dryopteris uliginosa* (Kunze) Christensen, *Index Fil.* suppl. III : 100 (1934).—*Thelypteris uliginosa* (Kunze) Ching in *Bull. Fan. meml Inst. Biol.* (Bot.) **6** : 342 (1936). Holttum, *Rev. Fl. Malaya* **2** : 241 (1955).

Polypodium tenericaule Hook. in *Hooker's J. Bot.* **9** : 353 (1857). Type: China, *Alexander* (K).—*Lastrea tenericaulis* (Hook.) Moore, *Index Fil.* : 99 (1858). Bedd., *Handb. Ferns Brit. Ind.* : 266 (1883).—*Nephrodium tenericaule* (Hook.) Hook., *Spec. Fil.* **4** : 142, excl. t. 269 (1862) p.p.—*Aspidium tenericaule* (Hook.) Thwaites, *Enum. Pl. Zeyl.* : 393 (1864).

Lastrea setigera sensu Bedd., *Ferns South. Ind.* Correct. p. i (1864) p.p., errore '*L. flaccida*' in t. 99 (1863), non *Cheilanthes setigera* Blume (1828).—*Nephrodium setigerum* sensu Hook. & Baker, *Syn. Fil.* : 284 (1867) p.p.—*Dryopteris setigera* sensu Christensen, *Index Fil.* : 292 (1905) p.p.

Rhizome short-creeping; *stipes glaucous* when fresh, stramineous when dry, short or long, base more or less fleshy and clothed with narrow, brown, hairy scales; distal parts of stipe and rhachis glabrous save in the grooved upper surface; *lamina bipinnate-pinnatifid or subtripinnate,* varying widely in size, in small fronds 20 × 12 cm in large fronds four times as big, deltoid-ovate in outline, the largest pinnae up to 30 × 15 cm acuminate, lower pinnules free the rest and those in upper part of frond adnate to a narrow wing on the pinna axis; pinnules acuminate divided to a narrow wing on each side of the costa, the segments oblong, blunt-ended, dentate to deeply lobed, glabrous above save for short, antrorse, white hairs on the raised costa, *lower surface of costae and costules bearing scattered, long, white, mostly multicellular hairs and whole undersurface sprinkled with short, capitate, gland-like hairs;* veins forked, not reaching the margins of the segments, distal parts thickened and conspicuous on upper surface; texture herbaceous; sori small, one to each lobe and slightly nearer to main vein than margin; indusia very small, membranous, usually bearing a few hairs.

Collections: Thwaites C.P. 1286 (BM; CGE; K; P; PDA.). *Thwaites* C.P. 1365 (PDA). Rambodde, on shady banks, June 1845, *Gardner* 1150 (BM; CGE; K). Kaduganawa, margins of forests, Oct. 1846, *Gardner* 1222 (CGE; K). Ramboda Pass, 960 m, 17 Dec. 1950, *Sledge* 656 (BM). Same locality, *c.* 925 m, 2 Jan. 1977, *Faden* 77/37 (K). Corbet's Gap, roadside through secondary jungle, 1290 m, 9 Dec. 1950, *Sledge* 572 (BM). Between Hakgala and Ambawela, 1650 m, 25 Dec. 1950, *Sledge* 788 (BM). Between Madugoda and Weragamtota, roadside bank through jungle, 750 m, 9 Jan. 1954, *Sledge* 949 (BM). Badulla, *Freeman* 259, 260, 261 (BM). Near Badulla, roadside bank, 29 Dec. 1950, *Sledge* 780 (BM). Near Urugala on Kandy-Mahiyangana road, *c.* 650 m, 24 Dec. 1976, *Faden* 76/561 (K). Opanaki, Kelani Valley near Ratnapura, bushy roadside bank, 5 Jan. 1951, *Sledge* 801 (BM). Manawella, 160 m, Sab. Province, Jan. 1954, *Schmid* 1067 (BM). Unlocalised: *Walker* (K). *Robinson* (K). *Mrs Chevalier* (BM). *Alston* E71 (PDA).

Plentiful in the interior in open grassy places or in light shade, from sea level to 1750 m.

Tropics of the Old World from Madagascar eastwards to southern China, Japan and Hawaii and southwards through India and Malaysia to north-eastern Australia and Polynesia. Adventive in New World.

Macrothelypteris torresiana is one of the commonest thelypteroid ferns in Ceylon. It varies widely in size, large fronds reaching two metres in height with stipes 120 cm long; the largest pinnae of such plants exceed the whole lamina of small plants, wherein only the lowest pinnae may be fully pinnate. Normally its subtripinnately dissected fronds bearing long, septate, hyaline hairs on the under surface of the pinnae are sufficient to distinguish it from all the other thelypteroid ferns. In the field it is easily recognised by its glaucous stipes. An insignificant indusium is normally present, but sometimes it is entirely lacking.

III. METATHELYPTERIS (H. Itô) Ching

in *Acta phytotax. sin.* **8** : 305 (1963).

Caudex usually erect; fronds small, pinnate with deeply lobed pinnae or bipinnate with adnate pinnules, lowest pinnae not or little reduced; upper surface of costae not grooved; veins free, often forked, not reaching the margins; lower surface of pinnae with unicellular, acicular and/or short capitate hairs also short multicellular reduced scales; sori indusiate, sporangia without hairs, spores dark with thick wings or raised bands. n = 31, 35, 36.

About 12 species: India and Ceylon to south China and Japan; Malesia; Solomon Islands and one species in São Tomé and Madagascar.

1. **Metathelypteris flaccida** (Blume) Ching

in *Acta phytotax. sin.* **8** : 306 (1963).—*Aspidium flaccidum* Blume, *Enum. Pl. Jav.*: 161 (1828). Type : Java, Burangrang, *Blume*.—*Lastrea flaccida* (Blume) Moore, *Index Fil.* : 92 (1858). Bedd., *Ferns South. Ind.* : t. 250 (1864); *Handb. Ferns Brit. Ind.* : 244 (1883).—*Nephrodium flaccidum* (Blume) Hook., *Sp. Fil.* **4** : 133, t.263 (1862); *Syn. Fil.* : 274 (1867).—*Dryopteris flaccida* (Blume) Kuntze, *Rev. Gen. Pl.* **2** : 812 (1891); Christensen, *Index Fil.* : 266 (1905).—*Thelypteris flaccida* (Blume) Ching in *Bull. Fan meml. Inst. Biol.* (Bot.) **6** : 336 (1936).

Rhizome erect, fronds tufted; stipes up to 30 cm long, slender, black at the base which is sparsely scaly, stramineous above, more or less hairy; lamina lanceolate or oblong-lanceolate 20–40 × 7·5–15 cm, pinnate with deeply pinnatifid pinnae; pinnae subopposite below and sometimes throughout, sessile, basal ones shortened and often deflexed, middle ones 5–10 × 1·5–2 cm, base truncate apex acuminate, *pinnatifid to a narrow wing between the pinnules*; pinnules oblong or linear-oblong, obtuse to subacute at the apex, cut about half way to the costa into 4–6 pairs of slightly falcate rounded lobes with ciliate margins; *rhachis hairy, winged in the distal part*; texture softly herbaceous; both sides of pinnae hairy, *the lower surfaces usually with many long spreading white hairs* especially on the costa, costules and veins but sometimes only sparsely hairy; *veins forked, not reaching the margins*; sori medial round, at or near the apex of an anterior veinlet, *indusium small,* membranous, margins *fringed with hairs.*

Collections: *Thwaites* C.P. 3802 (BM; CGE; K; P; PDA). *Thwaites* C.P. 1365 (BM; CGE; K; P) In woods at Nuwara Eliya, Sept. 1844, *Gardner* 1152 (CGE; K). Same locality: *Mrs Chevalier* (BM); *Freeman* 238, 239, 240, 241 (BM); 1950 m, 11 March 1954, *Schmid* 1506 (BM). Adams Peak, 14 Feb. 1905, *Matthew* (K). Same locality, north slope at 1950 m, 14 Dec. 1950, *Sledge* 622 (BM); *Moon* (BM). Peacock Hill, Pussilawa, *Beckett* 71 (BM). Corbets Gap, secondary jungle, 1320 m, 9 Dec. 1950, *Sledge* 569 (BM). Jungle between Pattipola and Horton Plains, 1950 m, 20 Dec. 1950, *Sledge* 672 (BM). Horton Plains, 2270 m, 7–8 March 1954, *Schmid* 1371 (BM). Hakgala, by jungle steam, 1650 m, 27 Dec. 1950, *Sledge* 743 (BM). Road between Hakgala and Nuwara Eliya, 1620 m, 27 Dec. 1950, *Ballard* 1267 (K). Moon Plains, Nuwara Eliya, wet ground in secondary jungle, 1800 m, 23 Dec. 1950, *Sledge* 718 (Bm). By the Ramboda Pass-Maturata track, 1890 m, 17 March 1954, *Sledge* 1352 (BM). Tonacombe Estate, Namunukula, 1350 m, 23 Feb. 1954, *Sledge* 1180 (BM). Near Ambawela junction on Hakgala-Pattipola road, on banks of streams and in roadside ditches, 2 Jan. 1977, *Faden* 77/20 (K). Unlocalised : *Walker* (K; P; PDA). *Wall* (K; P). *Robinson* 158 (K).

In the higher parts of the interior; frequent by steams and in damp ground in forests.

Southern India, Ceylon, northern India, southern China, and Java.

var. repens Sledge, **var. nov.**

A typo specie differt: rhizoma late repens, ramosum, frondibus plus minusve approximatis, stipitibus basibus curvatis.

Collections: Kandapola, nr. Nuwara Eliya, 1800 m, 19 March 1954, *Sledge* 1323 (BM, holotype). Horton Plains, road to World's End on roadside banks in forest, ±2090 m, 15 Nov. 1976, *Faden* 76/284 (K).

Thwaites (in *Enum. Pl. Zeyl.*: 393 (1864)) cites C.P. 1365 as *Aspidium tenericaule* (= *Macrothelypteris torresiana*); one of the PDA sheets and another at Paris so numbered are that species, but 12 other sheets examined are all *Metathelypteris flaccida.*

My Kandapola plants with wide-creeping and branching rhizomes are so entirely different in habit from the normal erect-growing plant that I assumed that they were specifically distinct. Faden's gathering from Horton Plains is clearly the same. I can find no character however which would serve to distinguish fronds detached from plants with creeping and erect rhizomes.

A parallel case is that of *Polypodium late-repens,* described by Trotter in Hope as a new species, largely on the basis of its wide-creeping habit as opposed to the erect-growing *P. distans* D. Don (= *Pseudophegopteris pyrrhorhachis*). However, Holttum (in *Blumea* **17**: 24 (1969)) does not recognise the taxon, even at a varietal level, on the grounds that he 'can see no distinction between specimens lacking rhizomes'. *Christella papilio* also has both creeping and erect forms, the detached fronds of which are likewise inseparable (*p.* 38).

Manton found both diploid and tetraploid plants of *Metathelypteris flaccida* in Ceylon, the tetraploid being collected at Horton Plains. I am unable to say however if the tetraploid plant had a creeping rhizome, as is the case in *Christella papilio.*

IV. AMAUROPELTA Kunze

in *Farnkr.* **1**: 86, 109, t.51 (1843).

Caudex erect or a few species with creeping rhizomes; fronds pinnate with deeply pinnatifid pinnae, decrescent below, attenuate upwards, aerophores often present at bases of pinnae ± swollen; veins simple, free, the basal ones passing to the margins above the base of the sinus between adjacent segments, sessile glands sometimes present on lower surface, short-stipitate, often coloured hairs and acicular or uncinate hairs also often present; sori usually supramedial, indusia small, often glandular or hairy, sometimes absent; sporangia short-stalked, bearing neither hairs nor glands; spores wingless with a very fine raised reticulum. $n = 29$.

About 200 species: mostly from tropical and subtropical America from Mexico to Chile and Northern Argentina; eight species in Africa, Madagascar and the Mascarene Islands and one in Hawaii. Not previously recorded from Asia.

1. **Amauropelta hakgalensis** Holttum, **sp. nov.** (Fig. 1)

'*A. bergianae* (Schlechtendal) Holttum et *A. oppositiformi* (Christensen) Holttum affinis; a priore differt: planta minore, pinnis inferioribus basi non angustatis, pagine inferiore pilis capitatis etiam pilis acicularibus hamatis intermixtis vestita; a posteriore differt: pinnis fere ad costam lobatis, pagina inferiore pilis hamatis praedita, glandulis subsessilibus rubris destituta.' (Holttum, *in litt.*).

Caudex short, erect; scales thin, to 7 × 1 mm, bearing a few capitate hairs. Stipe 8–15 cm long, with spreading pale hairs almost 1 mm long. Lamina 40 cm long, pinnae 16 pairs (P. 220 has lamina 62 cm, pinnae 23 pairs); about 6 pairs of lower pinnae gradually reduced and more widely spaced, lowest 3 mm long, base of upper reduced pinnae almost symmetrically truncate, not auricled. Largest pinnae 4·5 cm long, 1·3–1·5 cm wide at base (P. 220, 5·5 × 1·7 cm), evenly attenuate from truncate base to apex, lobed to within 0·5 mm from costa at base, less deeply distally, lobes not falcate, slightly oblique, edges of larger ones sinuate; costules 3 mm apart (P. 220 to 4 mm); veins 6–7 pairs (P. 220, 8–9 pairs); lower surface of rhachis with spreading pale hairs more than 1 mm long, of costae with similar hairs and shorter ones, distal shorter ones hooked, also short capitate hairs; *costules as costae with shorter hairs, some hooked*; veins and *surface between veins bearing short erect hairs, hooked and capitate*; upper surface of rhachis bearing pale spreading hairs 1 mm long, with shorter ones and capitate hairs in groove, costae with straight hairs 0·7 mm, veins and surface with sparse shorter acicular hairs, not hooked. Sori supramedial; *indusia very small* bearing a

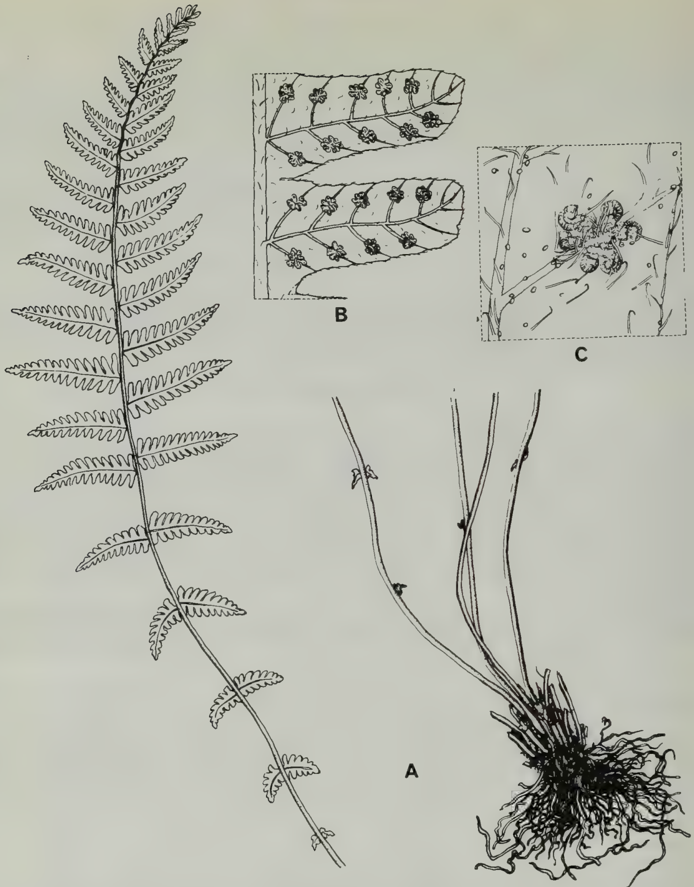

Fig. 1 *Amauropelta hakgalensis* Holttum: A–plant (*Holttum* S.F.N. 39169, holotype), × 0·5; B–part of pinna, × 8; C–under surface of pinna lobe to show sorus, acicular, hooked and capitate hairs, × 30.

few acicular and capitate hairs; spores typical of the genus with a complex fine two-dimensional reticulum.

Collections: Shrubby slopes above Hakgala Botanic Garden, 1670 m, 23 Dec. 1950, *Holttum* S.F.N. 39169 (SING, holotype; K, isotype). Same locality and date, cult. Kew, *I. Manton* P. 220 (BM). Hakgala Bot. Gardens and slopes of Hakgala Mt., 1720–1820 m, 14 Nov. 1976, *Faden* 76/272 (K).

Endemic? or possibly introduced, but not referable to any other known species of *Amauropelta.*

This is the fern recorded in Manton & Sledge (*Phil. Trans. R. Soc.* B, **238** : 137 (1954)) as 'P. 220 *Thelypteris n.sp.*'. Being still unable to match the material with any Indian or Malayan fern, specimens were sent to Dr Holttum who recognised it as a species of *Amauropelta*. No species of *Amauropelta* has hitherto been recorded from Asia, and since Holttum reported that the Hakgala fern does not agree with any of the few species known to occur in Africa, Madagascar or the Mascarene Islands, he has described the fern, at my invitation, as a new species. Meanwhile Dr Faden visited Ceylon and, at our request, searched for the new species on the hill slope above the Hakgala Botanic Garden and had little difficulty in refinding the plant in two or three widely separated localities. Its occurrence in the proximity of a Botanical Garden puts it under suspicion of being an introduced species, presumably from America, since it does not agree with any known species from the Old World. Accordingly, I sent a gathering to Alan R. Smith for examination and comment. After kindly comparing it with American species he replied that he was 'unable to match the Ceylon specimen with any known American sp. and I feel that there is a good *probability* that it is not American . . . I think there is a good case for describing your plant as new.'

The chromosome count given for this fern by Manton (in Manton & Sledge, *loc. cit.*) was inadvertently cited as 'n = 62' whereas the slip accompanying the voucher specimen from which the count was made reads 'n = *c.*60 (prob. 62)'. Dr Lovis obtained approximate counts from a fixing of a plant sent to Kew by Dr Faden which gave 57–59. The true number therefore is likely to be 58.

V. **PARATHELYPTERIS** (H. Itô) Ching

in *Acta phytotax. sin.* **8** : 300 p.p. (1963). Holttum in *Blumea* **19** : 32(1971).

Small ferns with slender creeping rhizomes; fronds pinnate with deeply pinnatifid pinnae, decrescent or not; veins free, reaching the margins, costae grooved on upper surface; lower surface of pinnae with sessile, spherical glands and often with slender, septate hairs; sori indusiate, capsules eglandular and without setae; spores opaque with a narrow irregular wing. n = 27, 31 [*c.* 36].

About 10 species: mostly from warmer parts of mainland Asia, to New Guinea, Solomon and Philippine Islands, and Japan.

1. **Parathelypteris beddomei** (Baker) Ching

in *Acta phytotax. sin.* **8** : 302 (1963).—*Nephrodium beddomei* Baker in Hook. & Baker, *Syn. Fil.* : 267 (1867). Type: Travancore, *Beddome* (?K, not seen).—*Lastrea beddomei* (Baker) Bedd., *Ferns Brit. Ind. Corr.*: 11 (1870); *Handb. Ferns Brit. Ind.* : 239 fig. 122 (1883).—*Dryopteris beddomei* (Baker) Kuntze, *Rev. Gen. Pl.* **11** : 812 (1891).—*Thelypteris beddomei* (Baker) Ching in *Bull. Fan. meml. Inst. Biol.* (Bot.) **6** : 308 (1936). Holttum, *Rev. Fl. Mal.* **2** : 240 (1955).

Lastrea gracilescens sensu Bedd., *Ferns South. Ind.* : 38, t.110 (1863), non *Aspidium gracilescens* Blume (1828), nec *Nephrodium gracilescens* (Blume) Hook. (1862). *Aspidium gracilescens* sensu Thwaites, *Enum. Pl. Zeyl.* : 391 (1864), non Blume (1828).

Rhizome long-creeping, sparsely scaly, fronds spaced, up to 50 cm long; stipes 5–15 cm, stramineous, naked or with a few scales at the base; *lamina* pinnate 20–30 × 4–6 cm, widest above the middle, tapering to the apex and *gradually narrowed downwards,* the lower pairs of pinnae becoming remote and much reduced in size, rhachis hairy above, minutely glandular-pubescent elsewhere; pinnae patent, cut almost to the costa into oblique mostly entire, obtuse or subacute segments, those adjacent to the rhachis often bluntly lobed, glabrous above save for short hairs on the costa, *lower surface bearing scattered, longish, white, acicular hairs* on the costa and veins and *sessile spherical glands*; texture firm-herbaceous; sori submarginal, indusia small, glandular.

Collections: Thwaites C. P. 1287 (BM; CGE; K; P; PDA). Newera Eliya, banks of streams in open places, Sept. 1844, *Gardner* 1141 (CGE). Nuwara Eliya, April 1899, *Gamble* 27585 (K). Same locality, 9 May 1906, *Matthew* (K). Same locality, Jan. 1908, *Bicknell* (P). Same locality, *Freeman* 231, 232, 233 (BM).

Same locality, Feb. 1954, *Schmid* 1298, 1363 (BM). Same locality at *c.* 1980 m, 2 Jan. 1977, *Faden* 77/34 (K). Sita Eliya, patana near river, 1740 m, Oct. 1897, *Pearson* 226 (CGE). Between Pattipola and Horton Plains, marshy ground by stream, 1800 m, 20 Dec. 1950, *Sledge* 668 (BM). Ramboda Pass—Maturata track, *c,* 1900 m, 17 March 1954, *Sledge* 1315 (BM).

In swampy places in the highest parts of the Central Province: frequent about Newara Eliya.

Southern India, Ceylon, Sumatra, Java and widely throughout Malaysia on mountains to New Guinea, Taiwan, Philippines, and south Japan.

VI. THELYPTERIS Schmidel

in Keller, *Icon. Pl.:* 45, t.11, 13 (1763).

Rhizome slender, long-creeping, growing in marshy ground; fronds pinnate with deeply pinnatifid pinnae, the basal ones not or little reduced; veins free, reaching the margins, costae grooved on upper surface, small, flat, thin scales present on lower surface of costae (also filamentous small ones) but sessile spherical glands absent; sori indusiate, short capitate hairs sometimes present on sporangia near annulus; spores spinulose. n = 35.

Four species: north temperate Europe and Asia and south tropical and subtropical Africa, Madagascar, southern India, Thailand, Sumatra, New Guinea, and northern New Zealand.

1. **Thelypteris confluens** (Thunb.) Morton

in *Contr. U.S. natn. Herb.* **38** : 71 (1967). Schelpe, *Fl. Zamb. Pterid.:* 190, tab. 55E (1970).—*Pteris confluens* Thunb., *Prodr. Pl. Cap.*: 171 (1800). Type: South Africa, *Thunberg* (UPS).

Aspidium thelypteris var. *squamigerum* Schlechtendal, *Adumbr. Fil. Prom. Bon. Spei* : 23, t.11 (1825). Type: South Africa, Cape Peninsula, *Schlechtendal* (HAL).—*Lastrea thelypteris* var. *squamigera* (Schlechtendal) Bedd., *Suppl. Handb. Ferns Brit. Ind.* : 54 (1892).—*Thelypteris palustris* var. *squamigera* (Schlechtendal) Weatherby in *Contr. Gray Herb. Harv. II,* **73** : 40 (1924).—*Thelypteris squamigera* (Schlechtendal) Ching in *Bull. Fan meml Inst. Biol,* (Bot.) **6** : 329 (1936) sub '*squamulosa.*'

Lastrea fairbankii Bedd., *Ferns Brit. Ind.*: 254 (1867); *Handb. Ferns Brit. Ind.*: 240 (1883). Type: southern India, Pulney Mts, *Beddome* (K).

Rhizome wide-creeping, black, sparsely scaly; stipes 20–30 (50) cm, stramineous, black at the base, glabrous; lamina 15–25 cm long, 5–8 cm wide, pinnate with deeply pinnatifid pinnae, broadly lanceolate or oblong in outline, basal 2–3 pairs of pinnae reduced in size and often more distant, rhachis glabrous or with scattered minute gland-like pubescence; pinnae cut almost to the costa into oblong acute or obtuse, entire lobes often with recurved margins, upper surface glabrous, *lower surface with ovate brown scales on the costa,* elsewhere glabrous to slightly pubescent on the midribs and veins, texture stiff, chartaceous; sori medial or nearer costules, indusium fimbriate at the margin.

Collections: Swamp near Bandarawella, Uva Province, in great abundance, Sept. 1890, [no collector's name] (PDA).

Africa south of the equator, Ethiopia and Sudan, Madagascar; southern India, Ceylon, Sumatra, mountains of New Guinea, and New Zealand (North Island).

The collection from Bandarawella, named *Lastrea beddomei,* is superficially similar to that species, but has much less markedly decrescent fronds which lack glands and white, acicular hairs on the under surface of the pinnae, but have ovate brown scales on the costas. The locality where these specimens were collected is likely to have been an area of open ground 3–5 km west of Bandarawella, and the fern probably still grows there since modern maps still indicate the presence of much swamp and marsh. The elevation is 1200 m, which is the same as that in the Pulney Mountains locality cited by Beddome for *L. fairbankii.*

VII. CYCLOSORUS Link

Hort. Reg. Bot. Berol. **2** : 128 (1833). Holttum in *Blumea* **19** : 27 (1971).

Rhizome long-creeping, growing in wet ground; fronds pinnate, pinnae pinnatifid, the lower ones not reduced; thin, flat scales present on lower surface of costae; upper surface of costae grooved; basal veins anastomosing, the next pair passing to sides of sinus; lower surface of pinnae usually bearing acicular and/or capitate hairs and sessile, red glands; sori indusiate, sporangium stalk bearing multicellular gland-tipped hairs, capsules eglandular, spores muricate. n = 36.

Three species: pan-tropical and subtropical.

1. **Cyclosorus interruptus** (Willd.) H. Itô

in *Bot. Mag., Tokyo* **51** : 714 (1937) *nomen tantum.—Pteris interrupta* Willd. in *Phytographia* **1** : 13, t.10, fig. 1 (1794). Type: southern India, *Klein* (B).

Aspidium obtusatum Swartz in *J. Bot. Göttingen* **1800** (2) : 33 (1801); *Syn. Fil.* : 248 (1806). Type: Java, *Thunberg* (BM).

Aspidium goggilodus Schkuhr, *Krypt. Gew.* **1** : 193, t.33c (1809). Type from Guyana.—*Cyclosorus gongylodes* (Schkuhr) Link, *Hort. Reg. Bot. Berol.* **2** : 128 (1833). Ching in *Bull. Fan meml Inst. Biol.* (Bot.) **8** : 186 (1938). Holttum, *Rev. Fl. Malaya* **2** : 261, fig. 148 (1955).

Nephrodium propinquum R.Br., *Prodr. Fl. Nov. Holl.* : 148 (1810). Hook., *Spec. Fil.* 4 : 49 (1862). Bedd., *Ferns South. Ind.* : 32, t.89 (1863). Type : Australia, *Banks* (BM).—*Aspidium propinquum* (R.Br.) Thwaites, *Enum. Pl. Zeyl.* : 391 (1864).

Nephrodium unitum sensu Bedd., *Handb. Ferns Brit. Ind.* : 268 (1883), non *Polypodium unitum* L. (1759).

Rhizome creeping; stipes about 50 cm long, black at the base, brown distally, glabrous save about the base which bears scattered brown scales when young; lamina 30–60 cm pinnate with up to 25 pairs of pinnae, *the lowest pair not or scarcely reduced,* apex of frond pinna-like; largest pinnae up to 15 × 1·5 cm apex acute, base truncate or broadly cuneate, *cut down about one third into deltoid lobes* with rounded sides and acute apex; veins 6–10 pairs per lobe, the lowest veins of adjacent lobes anastomosing forming an excurrent vein which is often joined by the next acroscopic vein beneath the sinus; lower surface of costae with scattered broad scales, *the costules and veins bearing sessile, spherical, reddish or orange glands,* otherwise both surfaces glabrous (in Ceylon plants) save for some ciliate hairs on the margins; textures chartaceous; sori medial on the veins, absent from the lowest pair, indusia glabrous or with a few hairs.

Collections: Thwaites C.P. 705 (BM; CGE; K; P; PDA). Colombo, coll. *Randall* 1870, 1871, *Rawson* 3245 (BM). Caltura, *Macrae* 217 (CGE; E; K; P). Galle, *Freeman* 262 (BM). Tamankaduwa, 1893, *Nevill* (PDA). Near Ratnapura, marshy ground by road, 3 Jan. 1951, *Sledge* 798 (BM). Marsh near Bentota, Western Province, 19 Jan. 1951, *Sledge* 880 (BM). Unlocalised: *Barkly* 14, 16 (BM). 1839, *Mackenzie* (K). *Skinner* (K). *Ferguson* (US).

Open, marshy places at low elevations in western and southern parts of Ceylon.

Tropical and subtropical Africa, Madagascar; India eastwards to China, Japan and the Philippines, and south through Malesia to New Zealand; Polynesia; tropical America including Brazil.

An exclusively low altitude fern; the only other thelypteroid ferns in Ceylon which are also confined to low elevations are *Ampelopteris prolifera, Trigonospora glandulosa* and *T. zeylanica.*

The under surfaces of the pinnae seem always to lack hairs in Ceylonese specimens. In other parts of its very wide range they vary from glabrous to densely villous. Mettenius created the varieties *glabrum* and *hirsutum* to cover such variation and Ching has upheld them. Others have not done so because there appears to be a continuum between the two extremes.

VIII. AMPELOPTERIS Kunze

Bot. Ztg. **6** : 114 (1848).

Rhizome wide-creeping; fronds of indefinite apical growth proliferating from buds borne distally on the rhachis; forked unicellular hairs present on rhachis; pinnae subentire, most veins from adjacent costules anastomosing; sori exindusiate, round or somewhat elongate, hairs on stalks of sporangia bearing a terminal glandular cell. n = 36.

A monotypic genus distributed throughout the wetter parts of tropical and subtropical regions of the Old World.

1. **Ampelopteris prolifera** (Retz.) Copel.

Gen. Fil. : 144 (1947).—*Hemionitis prolifera* Retz., *Obs. Bot.* **6** : 36 (1791). Type : southern India *Koenig* (GOET)—*Meniscium proliferum* (Retz.) Swartz, *Syn. Fil.* : 19. 207 (1806). K. Iwats. in *Mem. Coll. Sci. Kyoto Univ.* B, **31** : 196 (1965).—*Goniopteris prolifera* (Retz.) C. Presl, *Tent. Pterid.* : 183 (1836). Bedd., *Ferns South. Ind.* : t.172 (1864); *Handb. Ferns Brit. Ind.* : 296, fig. 153 (1883).—*Dryopteris prolifera* (Retz.) Christensen, *Index Fil.* : 286 (1905).
Ampelopteris elegans Kunze in *Bot. Ztg.* **6** : 114 (1848). Origin unknown.

Rhizome creeping, sparsely scaly, stipes close together; fronds pinnate *some pinnae bearing axillary buds* which may remain dormant or may form tufts of secondary fronds; *fronds of two kinds, some* 30–60 cm long, *imparipinnate* with up to 10 pairs of pinnae, *others of indefinite apical growth, arching over and rooting at or near the tip,* their distal pinnae much shortened; pinnae up to 15 cm long, 1–1·75 cm broad, subsessile with truncate base and acute apex, becoming obtuse in the shortened distal pinnae, *margins crenate or subentire*; veins up to 10 pairs, 4–6 pairs uniting to form a sinuous excurrent vein; *rhachis bearing some unicellular forked hairs*; costa hairy above and with a few ciliate scales beneath, veins with scattered hairs on lower surface; texture firm-herbaceous; *sori oblong or elongate,* becoming confluent in age, *exindusiate.*

Collections: Thwaites C.P. 3916 (PDA). Tamankaduwa District, near Matale boundary, 1893, *Nevill* (PDA). Minnery, *Beckett* 1131 (PDA). Uma-Oya, in water, 1881, [no collector's name] (PDA). Kannia, hot wells, Dec. 1885, *W. F[erguson]* (PDA). Hot wells close to Trincomalee, *Freeman* 295, 296 (BM). Kannia Hot wells near Trincomalee, in marsh, 16 Jan. 1951, *Sledge* 879 (BM).

Rare in Ceylon, all localised records are on the eastern side of the central massif at low elevations.

Widespread in the tropics of the Old World from Africa to New Caledonia.

A marsh species growing in open places or in light shade. Those fronds which have indefinite apical growth produce shortened pinnae and such fronds always seem to remain sterile.

IX. TRIGONOSPORA Holttum

in *Blumea* **19** : 29 (1971).

Caudex erect; basal pinnae not or little shortened and never reduced to auricles on the stipe, pinnae usually deeply lobed; veins free the basal acroscopic one running to the base of the sinus between two segments, the basal basiscopic one reaching the edge above the base of the sinus; sori indusiate; spores trilete, minutely papillose. n = 36.

Trigonospora is unique amongst thelypteroid ferns in having trilete spores. All species commonly grow amongst stones in or close by river beds. The genus is confined to south-eastern Asia and was estimated by Holttum (in Blumea *loc. cit.*) to contain about eight species with the probability of some other species awaiting description. Over most of its area of distribution the species are clearly defined (and often very uniform), but in southern India and Ceylon, the degree of variability reaches its maximum and the species are, in consequence, more difficult to distinguish. This diversity led Hooker and Thwaites to include all plants from there within one variable species which they identified as Blume's Javan plant *Aspidium calcaratum.* Beddome recognised a number of different variants which he treated as varieties under *Lastrea calcarata* (Blume) Moore.

I believe that most Ceylon specimens can be referred readily to one or other of the species enumerated below. Of these species, two are widely distributed in Ceylon, and the great majority of specimens in herbaria are referable to them. *Trigonospora glandulosa* is very distinct but is so far only known from a single gathering; *T. angustifrons,* which is also rare, is readily distinguished from *T. calcarata* but, nevertheless, its relation to that species requires further investigation; the identity of specimens referred to *T. ciliata* (Benth.) Holttum is more problematical.

Incomplete specimens, such as isolated fertile fronds, are sometimes difficult to name with confidence, and a few gatherings appear to be intermediates with mixed characters. Whether these are indicative of introgression can only be decided by experimental work. One of my gatherings (*Sledge* 752) differs from all others in having numerous forked veins with occasional anastomoses occurring between them in the pinna segments of the sterile frond; also present are a few small subsessile, colourless, clubbed hairs or glands on the veins beneath. These characters are most readily accounted for as a consequence of hybrid origin, the other parent being presumably *Christella parasitica.* No spores are present on the fertile frond but this may be due to age. Two gatherings in the British Museum, one of them collected by Moon in Ceylon, are also remarkable for the numerous proliferating buds in the axils of the pinnae. Further cytotaxonomic and cultural, as well as field observations are required before definitive conclusions as to the relationships can be established.

Key to species of Trigonospora

1	Base of pinnae truncate with pinna lobes close to rhachis		2
–	Base of pinnae cuneate with no pinna lobes close to rhachis	7. **T. zeylanica** (p. 24)	
2(1)	Lower surface of pinnae & indusia eglandular		3
–	Lower surface of pinnae & indusia glandular	6. **T. glandulosa** (p. 23)	
3(2)	Basal acroscopic lobes free at least in lower pinnae, lobes very oblique, indusia glabrous		4
–	Basal acroscopic lobes not free, lobes oblique, indusia hairy or glabrous		5
4(3)	Lamina 2–3 times as long as wide, pinnae oblong, hairy at least on the costae	4. **T. calcarata** (p. 21)	
–	Lamina 3–6 times as long as wide, pinnae fusiform, quite glabrous	5. **T. angustifrons** (p. 23)	
5(3)	Pinnae 4 cm or less, cut ½ way to costa, tips blunt or acute	3. **T. ciliata** (p. 20)	
–	Pinnae 4 cm or more, cut ⅔ or more to costa, tips acuminate or caudate		6
6(5)	Pinnae 4–8 cm long with about 10 pairs of lobes	2. **T. obtusiloba** (p. 18)	
–	Pinnae 8–13 cm long with 15–20 pairs of lobes	1. **T. caudipinna** (p. 15)	

1. **Trigonospora caudipinna** (Ching) Sledge, **comb. nov.** (Fig. 2A)

Thelypteris caudipinna Ching in *Bull. Fan meml Inst. Biol.* (Bot.) **6** : 288 (1936). Type: Hainan, *Hancock* 108 (K).—*Pseudocyclosorus caudipinnus* (Ching) Ching in *Acta phytotax. sin.* **8** : 324 (1963).

Aspidium ciliatum Wall. *Numer. List.* : 351 (1829) *nom. nud.—Nephrodium ciliatum* C. B. Clarke in *Trans. Linn. Soc.* (Bot.) II, **1** : 514 (1880) p.p., *nom., illeg.,* excl. *Lastrea sericea* sensu Bedd.—*Thelypteris ciliata* sensu Ching in *Bull. Fan meml Inst. Biol.* (Bot.) **6** : 289 (1936) p.p., excl. *Aspidium ciliatum* Wall. ex Benth. and *Lastrea sericea* sensu Bedd.—*Pseudocyclosorus ciliatus* sensu Ching in *Acta phytotax. sin.* **8** : 324 (1963) p.p.

Aspidium canum Wall. *Numer. List* : 387 (1829) *nom. nud.—Lastrea cana* J.Sm., *Cat. Cult. Ferns* : 57 (1857) p.p., *nom. nud.—Thelypteris cana* Ching in *Bull. Fan meml Inst. Biol.* (Bot.) **6** : 291 (1936) p.p.

Lastrea falciloba Bedd., *Ferns S. Ind.* : 37, t.105 (1863), non *Nephrodium falcilobum* Hook. Type: Anamallays, 3000′, *Beddome* (K).

Lastrea bergiana sensu Bedd., *Ferns S. Ind. & Brit. Ind. suppl.*: 16 t.370 (1876), non *Polypodium bergianum* Schlechter.

Lastrea calcarata var. *ciliata* Bedd., *Handb. Ferns Brit. Ind.* : 235, fig. 121 (1883)

Trigonospora ciliata var. *angustiloba* Holttum in Saldanha & Nicolson, *Fl. Hassan Dist. Karnataka, India* : 866 (1976). Type from southern India.

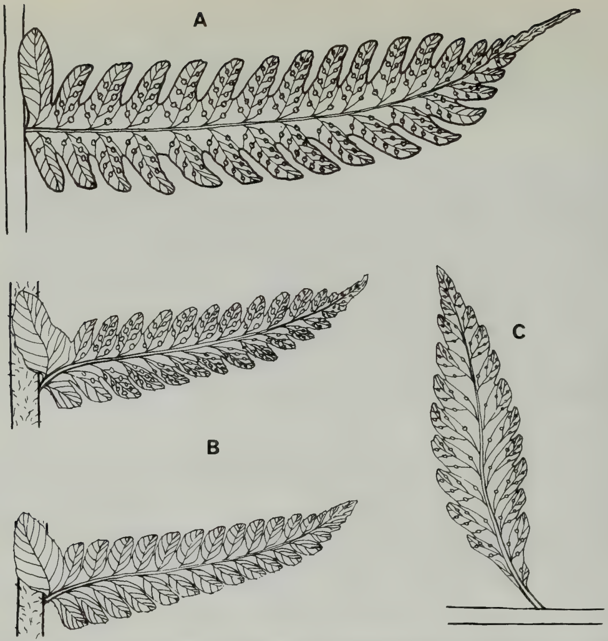

Fig. 2 Pinnae: A–*Trigonospora caudipinna* (Ching) Sledge *(Sledge* 1341), × 1; B–*T. ciliata* (Wall. ex Benth.) Holttum (*Sledge* 710), fertile and sterile, × 1·5; C–*T. zeylanica* (Ching) Sledge (*Sledge* 812), × 1·5.

Caudex erect, fronds up to 1 m long. Lamina 30–40 (–60) × 15–20 (–25) cm, broadly oblong to ovate-oblong with 15–20 pairs of free, sessile pinnae, the lowest pair usually deflexed and somewhat narrowed at the base at least on the basiscopic side. Pinnae pinnatifid to 2/3 or more, 8–13 × 1·5–2 (2·5) cm with 15 or more pairs of rounded lobes 3–4 (5) mm wide, the *basal acroscopic lobes* sometimes more deeply cleft but not, or very rarely, free to the base, often enlarged with forked veins and usually incurved close to or underlying the rhachis, *apex of pinnae with attenuate or caudate, entire tips 1–2 (3) cm long*; costa, costules and veins usually sparsely hairy beneath, margins with scattered hairs, surfaces glabrous or nearly so. Indusia glabrous or hairy.

Collections: Thwaites C.P. 1363 (CGE; K; P; PDA). Rambodde, shady banks, June 1845, *Gardner* 1107 (BM; CGE; K). *Gardner* 49 (P). Hantane, 1868, *Robinson* 156 (K). Yelumali, Namunukula, 12 March 1907, *J. M. Silva* (PDA). Mawanella, Sab. Province, 27 Jan. 1954, *Schmid* 1070 (BM). Ramboda Pass—Maturata track, *c.* 1900 m, 17 March 1954, *Sledge* 1303 (BM). Hakgala, edge of forest, 1800 m, 20 March 1954, *Sledge* 1341 (BM).

Moist banks especially by streams mainly in mountain forests.

South India, Ceylon, Nepal, Sikkim, Assam, Burma and China (Hainan Dao).

The type sheet of *Thelypteris caudipinna* Ching at Kew carries two detached fronds. These are 56 and 39 cm long, with laminas 28 and 23 cm long respectively; the pinnae are up to 9 × 1·5 cm long, with rather broad oblique lobes and with caudate apices 2–3 cm in length on the larger frond, but not exceeding 1–2 cm on the second frond. The basal pair of pinnae is deflexed, and the basal acroscopic segments of the pinnae are slightly enlarged and incurved to the rhachis. The indusia are sparsely hairy on one frond, but glabrous or with only occasional hairs on the other.

Apart from the exaggeratedly caudate tips to the pinnae on one of these fronds, the specimens match many gatherings from northern and southern India and Ceylon. Comparable specimens from India and Ceylon all have attenuate to caudate, entire tips to the pinnae, not infrequently reaching 2 cm in length. Since the presence of even longer caudate apices in one only of the type specimens is not consistently linked with any other characters which cannot be found in many other gatherings, this feature is evidently no more than an extreme development in an individual specimen, and cannot be regarded as of specific significance. Further evidence that Hancock's gathering from Hainan represents an abnormally developed specimen is provided by the fact that it has remained the only gathering in the *Thelypteris caudipinna* folder at Kew and no other collection is known to exist.

John Smith's *Lastrea cana*, later validated by Ching as *Thelypteris cana*, is the same species, as judged by three sheets in Smith's herbarium at the British Museum. Each sheet carries three detached fronds. Holttum has identified a frond on one sheet as *Amauropelta bergiana* (Schlechtendal) Holttum, but the other eight are all fertile fronds of a large species of *Trigonospora*, mostly with about 20 pairs of pinnae. These specimens match the fronds in Wallich's collection named *Aspidium ciliatum* (*Wall.* 351) and *A. canum* (*Wall.* 387), and they agree much more closely with Hancock's Hainan fern and Beddome's specimen from southern India than with Bowring's type specimen of *Trigonospora ciliata* (Benth.) Holttum from Hong Kong. The latter is a small fern with fronds 17·5–22·5 cm in length, the pinnae are without caudate or acuminate tips and the largest measure 4·5 × 1 cm. Part of the confusion which has prevailed between *T. caudipinna* and *T. ciliata* can be ascribed to the inexplicable statement in *Hooker's J. Bot.* **9** : 338 (1857) that the Hong Kong plant 'entirely agrees' with Wallich's Himalayan plants, when in fact they are notably different. This misleading statement was accepted by Ching (*loc. cit.* : 290) whose *T. ciliata* is a mixture of the two species.

I have been unable to discover on what grounds Ching stated that the type of *Thelypteris cana* was a gathering by Wight from south India. Smith cited no specimens, gave the provenance simply as East Indies, and none of his specimens at the British Museum were gathered by Wight. Ching implied that *T. cana* was a south Indian species but this is refuted by one of John Smith's sheets carrying specimens from Nepal, whilst both the synonyms cited by Ching were based on gatherings from north India. The three sheets named *Lastrea cana* by Smith are from: (a) Nepal: *Wallich and Hamilton*, (b) Madras: *Hook. fil. & Thomson* 249, and (c) Ceylon: *Gardner* 1107. The second of these sheets, the one on which all three fronds are clearly conspecific (though none has the 'densely hirsute' indusia indicated by Ching), is here chosen as the lectotype.

Beddome's specimen from the Anamallay Hills, from which was prepared his illustration of *Lastrea falciloba* (later, in his *Handbook*, named *L. calcarata* var. *ciliata*), is the same as the Hainan plant. It has a lamina 48 × 20 cm, pinnae up to 10 × 2 cm with markedly caudate apices and 15 or more pairs of pinna segments, 3 mm wide. The indusia are hairy. Ching (*loc. cit.* : 298) was incorrect in referring Beddome's illustration to *Thelypteris falciloba* (Hook.) Ching (later renamed *Pseudocyclosorus falcilobus* (Hook.) Ching), for Beddome specifically refers in the description in his *Handbook* to the absence on the stipe, in contrast to his var. *falciloba* which is 'furnished with auricles below the frond.' Large plants, closely similar to Beddome's specimen, occur in Sikkim, Assam and Burma and doubtless over the intervening region to Hainan. In Ceylon they are less common than the smaller *Trigonospora obtusiloba*, and localised specimens mostly come from high altitudes. *Robinson* 156

(K) closely matches the type of *T. caudipinna,* differing only in the shorter caudate tips to the pinnae.

Clarke's specimens of *Nephrodium ciliatum* and his description of the common form in Khasia as having caudate pinnae leave no doubt that *Trigonospora caudipinna* was the species intended. He correctly treated *Lastrea bergiana* sensu Bedd. as the same species. Although this is without reduced pinnae or auricles on the stipe, in his *Handbook,* Beddome later equated the species with Baker's *L. cana* in which the fronds are decrescent with auricled stipes. Beddome's own illustration of *L. cana* (in *Ferns Brit. Ind.*: t.307) depicts these characters, and is markedly different from his illustration of *L. bergiana,* although both illustrations are cited in the *Handbook* (p. 239) as portraying the same species. Clarke included *L. sericea* Scott ex Bedd. as a synonym of his *Nephrodium ciliatum.* This is similar in stature to *Trigonospora caudipinna* from which it differs in its short, wide and blunt pinnae. In other respects it does not vary significantly from *T. caudipinna,* to which it is certainly closely related. It should perhaps be regarded as a variant; however, such a treatment would necessitate the substitution of the earlier *sericea* for *caudipinna* as the specific epithet of the collective species.

Holttum's *Trigonospora ciliata* var. *angustiloba,* described as having 'frondibus multo majoribus, pinnis acuminatis' and identified with Beddome's illustration in *Ferns S. India* and the *Handbook,* is also *T. caudipinna.* The reason for the author's choice of epithet is not clear as there is no reference to the lobes of the pinnae being narrow in the type description.

2. **Trigonospora obtusiloba** Sledge, **sp. nov.** (Fig. 3)

Caudex erectus. Frondes usque ad 50 cm longae, fertiles stipitibus longis. Lamina in ambitu oblonga, ovata-oblonga vel deltoidea-ovata, plerumque cum 7–10 sed usque ad 15 paribus pinnarum liberarum sessilium, infimas deflexes basi contractas. Pinnae steriles (3) 4–6 (8) × 1–2 cm pinnatifidae ad 2/3, circa 10 paribus segmentorum subpatentium vel parum obliquorum, latorum, obtuse rotundatorum usque ad 5 mm latorum; frondes fertiles pinnis segmentisque angustioribus, segmenta basalia acroscopica plerumque aliquantum aucta, incurvata et saepe subter rhachides inflexa sed interdum vix ceteris dissimilia; pinna apice integra, acuta vel acuminata; costae, costulaeque venae subter pilis numeris variis, paginae subglabrae. Indusia plerumque hirsuta, interdum sparsissima vel glabra.

Caudex erect; *fronds up to 50 cm, the fertile ones with long stipes.* Lamina oblong, ovate-oblong or deltoid-ovate in outline, commonly with 7–10 but up to 15 pairs of free sessile pinnae, the lowest pair deflexed and contracted at the base. *Sterile pinnae* (3) 4–6 (9) × 1–2 cm, pinnatifid to 2/3 *with about 10 pairs* of subpatent or *slightly oblique, broad and bluntly rounded segments up to 5 mm wide*; fertile fronds with narrower pinnae and segments; basal acroscopic segments usually a little enlarged, incurved and often underlying the rhachis but sometimes scarcely different from the rest; pinnae apex entire, acute or acuminate; costa, costules and veins with variable amounts of hair below, surfaces subglabrous. Indusia usually hairy, sometimes very sparsely so or glabrous.

Collections: Adam's Peak, 14 Feb. 1908, *Matthew* (K; P). Same locality, at 1800 m, 14 Dec. 1950, *Sledge* 609 (BM). Nuwara Eliya, 1800 m, 10 May 1906, *Matthew* 622 (K). Same locality at 1980 m, 2 Jan. 1977, *Faden* 77/181 (K). Kuda Oya on Ramboda road, 1650–1700 m, 28 Dec. 1950, *Ballard* 1291 (K). Hakgala, 1800–1900 m, 27 Dec. 1950, *Sledge* 754 (BM). Sudagalla, 1050 m, 2 Feb. 1891, *Hancock* 22 (K). Riverstone Estate, Matale District at 1100 m, 19 Jan. 1977, *Faden* 77/181 (K). Ratnapura District, near stream, 750 m, 16 Nov. 1976, *Faden* 76/309 (K). Pahale Hewessa, near stream in jungle, 45 m, 20 Jan. 1951, *Ballard* 1527 (K); *Sledge* 889 (BM). Sinha Raja Forest near Hedigala, 75 m, 5 Jan. 1951, *Ballard* 1393 (K); *Sledge* 814 (BM, holotype). Sinha Raja Forest above Beverley Estate, Deniyaya, by stream 900 m, 12 March 1954, *Sledge* 1287 (BM). Kottawa Forest Reserve, 21 Jan. 1951, *Ballard* 1536 (K). Same locality, 60 m, 1 April 1954, *Sledge* 1378 (BM), Near Udagama near stream in jungle, 90 m, 21 Jan. 1951, *Sledge* 907 (BM). Kotmalee, 1847, *Fortescue* (CGE). Unlocalised: 'Ceylon 4000 ft.', *Beddome* (K). *Wall* spec. in herb. Blanford ex herb. C. W. Hope (P). *Walker* (K). *Gardner* 1363 (K). *Gardner* 1107 partim (CGE).

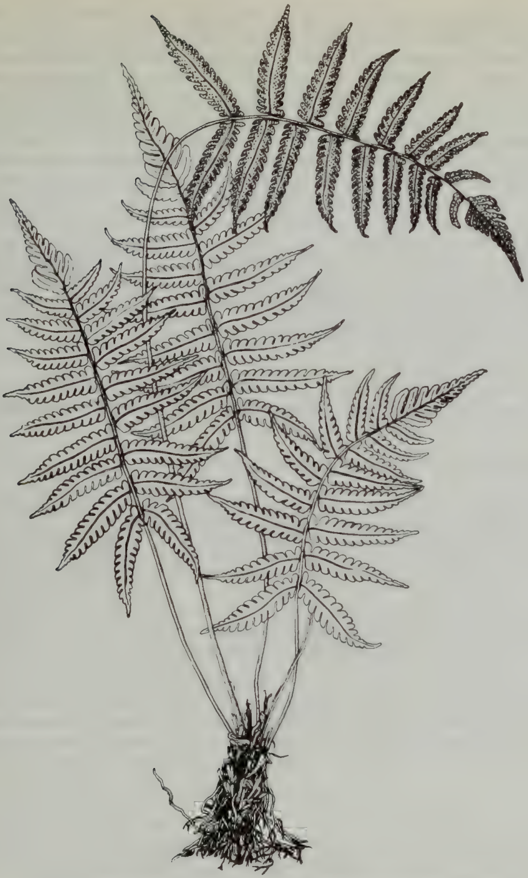

Fig. 3 *Trigonospora obtusiloba* Sledge: plant (*Sledge* 814), × 0·4.

By rivers and streams on shaded ground at all elevations up to 2000 m.
Known only from Ceylon.

This is the commonest species of *Trigonospora* in Ceylon. It is characterised by the marked distinction between sterile and fertile fronds, the latter having conspicuously longer stipes, often twice the length of the lamina and overtopping the sterile fronds. The sterile fronds have broad pinnae the segments of which are wide and rounded, the basal pair being deflexed and contracted at the base, at least on the basiscopic side. The fertile fronds have much narrower pinnae and pinna-segments, but fronds with broad pinnae similar to those of the sterile fronds with the segments bearing scattered sori are also produced; such fronds rarely, if ever, produce sori on each of the paired veins of the pinna segments, as in typical, fully fertile fronds. Sometimes the tips of the pinnae are long-attenuate or even caudate as in *T. caudipinna*, though *T. obtusiloba* is always a smaller species. The narrower fertile pinnae, and hence reduced size of the pinna segments in *T. obtusiloba,* results in the segments not being broadly rounded as in the sterile fonds; large detached fertile fronds of *T. obtusiloba* are therefore not easily distinguished from small fertile fronds of *T. caudipinna.* One of the difficulties in naming the species of *Trigonospora* lies in the fact that many gatherings consist only of detached fertile fronds, thus the valuable information afforded by comparison with sterile fronds from the same plant is not available.

Trigonospora obtusiloba and *T. caudipinna* have not previously been distinguished from one another. Both are usually labelled *T. ciliata* or *T. calcarata* var. *ciliata* in herbaria. Although Beddome's *Lastrea calcarata* var. *ciliata* was based on a large plant—originally named *L. falciloba*—which I consider to be identical with Ching's *Thelypteris caudipinna,* he later failed to distinguish between this and *T. obtusiloba* for there is a gathering of the latter from Ceylon named *L. calcarata* var. *ciliata* by him at Kew.

Trigonospora obtusiloba bridges the gap in size between *T. caudipinna* and *T. ciliata,* and this has doubtless contributed to the confusion between the two species. In *T. ciliata* the pinnae are less deeply lobed, the lobes of the sterile pinnae are never so broad and blunt, and the tips of the pinnae are usually acute, sometimes shortly acuminate, but never caudate.

3. **Trigonospora ciliata** (Wall. ex Benth.) Holttum (Fig. 2B)

in *Blumea* **19** : 29 (1971).—*Lastrea ciliata* Hook. in *Hooker's J. Bot.* **9** : 338 (1857), *nom. illeg.,* non *L. ciliata* Liebm. (1849).—*Aspidium ciliatum* Wall. ex Benth., *Fl. Hong Kong*: 455 (1861). Type: Hong Kong, *Bowring* 25 (K).—*Dryopteris ciliata* (Wall. ex Benth.) Christensen ex Wu, Wong & Pong in *Bull. Dept. Biol. Coll. Sci. Sun Yatsen Univ.* **3** : 30, pl. 6 (1932).—*Thelypteris ciliata* (Wall. ex Benth.) Ching in *Bull. Fan meml Inst. Biol.* (Bot.) **6** : 289 (1936) p.p. excl. *Aspidium ciliatum* Wall. *nom. nud., Lastrea sericea* sensu Bedd., and *Nephrodium ciliatum* C. B. Clarke *nom. illeg.*—*Pseudocyclosorus ciliatus* (Wall. ex Benth.) Ching in *Acta phytotax. sin,* **8** : 324 (1963) p.p.

Dryopteris pseudocalcarata Christensen, *Index Fil. Suppl.* **3** : 95 (1934) p.p., excl. *Aspidium ciliatum* Wall. *nom. nud., Lastrea sericea* sensu Bedd., and *Nephrodium ciliatum* C. B. Clarke *nom. illeg.*

Caudex erect; fronds up to 40 cm, the fertile ones with long stipes. Lamina oblong with up to 15 pairs of free pinnae, the lowest pair usually not deflexed. Sterile pinnae about 4 × 1 cm, *pinnatifid half way to the costa* with about 10–12 pairs of oblique, falcate segments, the basal acroscopic ones enlarged and incurved; apex of pinnae entire, acute or acuminate, costa, costules and veins hairy. Indusium (in Ceylonese specimens) naked or with sparse hairs.

Collections: Pas Dun Corle, Aug. 1865, *Thwaites* C.P. 992 (P). Between Hakgala and Nuwara Eliya, moist ground by track through jungle, 1650 m, 23 Dec. 1950, *Sledge* 710 (BM), *Holttum* 39161 (SING).

Very rare, or possibly overlooked; the absence of specimens in herbaria suggests the former.

South China and Thailand westwards to north-east India and southwards to northern Malaysia, Sumatra and Ceylon.

The type of *Trigonospora ciliata,* which is from Hong Kong, is considered by Holttum (see *Reinwardtia* **8** : 503–507 (1974)) to agree well with Malayan material. North India was also included in its distribution by both Holttum and Ching, although I have seen no specimen from this area which matches the Hong Kong or Malayan plants.

The first two collections cited above are not closely similar but are best referred to *Trigonospora ciliata.* Neither could be included in any other Ceylonese species. My own gathering (no. *710*) closely resembles the Hong Kong type in size and form. It differs, however, as does Thwaites' specimen of C.P. 992 at Paris (which is manifestly different from other gatherings bearing the same number), in having indusia which are either glabrous or only have very few hairs; in the type the indusia have abundant, long, setose hairs. However, not all specimens referred to this species are similarly clothed; Holttum (*loc. cit.*) described the indusia as 'very hairy' but in his description of Malayan plants they are alluded to as only 'ciliate.' There are considerable differences also in the degree of hairyness and length of hairs on the fronds of specimens referred to *T. ciliata.* Since plants of *T. caudipinna* may have densely hairy, sparsely hairy, or glabrous indusia, I do not believe that the presence or absence of hairs on the indusia is of significant taxonomic importance in the species of *Trigonospora.* Even in *T. calcarata,* in which the indusia are nearly always glabrous, I have seen specimens in which some hairs are present on the indusia.

The plants recorded as *Thelypteris ciliata* (Wall.) Ching by Manton & Sledge (*Phil. Trans. Roy, Soc. Lond.* B, **238** : 137, 1954) were probably *Trigonospora obtusiloba.*

4. **Trigonospora calcarata** (Blume) Holttum (Fig. 4B)

in *Reinwardtia* **8** : 506 (1974). *Aspidium calcaratum* Blume, *Enum. Pl. Jav.* : 159 (1828). Type: Java, *Blume* (L).—*Lastrea calcarata* (Blume) Moore, *Ind. Fil.* : 87 (1858).—*Nephrodium calcaratum* (Blume) Hook., *Spec. Fil.* **4** : 93 (1862) p.p.—*Dryopteris calcarata* (Blume) Kuntze, *Rev. Gen. Pl.* **2** : 812 (1891).—*Thelypteris calcarata* (Blume) Ching in *Bull. Fan meml Inst. Biol.* (Bot.) **6** : 288 (1936).

Caudex erect. Fronds up to 40 cm long, stipes hairy or glabrescent save in the groove, those of the fertile fronds longer than those of the sterile ones. Lamina oblong or ovate-oblong, up to 12 cm wide and 2–3 times as long with 10–13 pairs of free pinnae below the pinnatifid apex, the lowermost pair usually not deflexed. Pinnae oblong 4–7 × 0·75–1·0 cm, rarely larger, *pinnatifid from $\frac{2}{3}$ to $\frac{3}{4}$ to the costa* with up to 12 pairs of *narrow, very oblique, falcate segments,* 1·5–3 mm. wide, *the basal acroscopic segments at least in the lower pinnae quite free to the base* (or rarely very nearly so), erect and often a little elongated and lying close to the rhachis, the second pair of segments also sometimes free to the base, these and the remaining segments very oblique, pinna apex acute or shortly attenuate, entire; surfaces glabrous above save on the costa, subglabrous or with scattered rather long hairs on the costa and veins below. Indusia glabrous.

Collections: Thwaites C.P. 1363 (P, partim; PDA, partim). *Thwaites* C.P. 3273 (BM; CGE; K; P; PDA, partim). Moist woods at the foot of Adam's Peak, March 1846, *Gardner* 1250 (CGE; K). Foot of Adam's Peak, Carney near Ratnapura 240 m, 9 March 1954, *Sledge* 1246A (BM). Kitulgala, amongst rocks by riverside [low alt.], 28 Aug. 1927, *Alston* 897 (PDA). Deniyaya, Southern Province, 550 m, 5 Feb. 1954, *Schmid* 1138 (BM). 3–4 miles east of Madugoda, Central Province, amongst stones in stream in jungle, 750 m, 8 Jan. 1954, *Sledge* 937 (BM). Hunnasgiriya, Central Province, in stream bed amongst rocks in jungle, 870 m, 16 Jan. 1954, *Sledge* 981 (BM). Gallebodde, by stream in jungle 600 m, 26 Jan. 1954, *Sledge* 1042 (BM).

Stony ground by or in river beds in shade at low or moderate elevations.

Sumatra, Java and Ceylon.

The distinctive characters of *Trigonospora calcarata* are the deeply divided pinnae with very oblique segments, the basal segments normally (and sometimes the second pair also) being quite free down to the costa and often having a small lobe at the base. The indusia are almost always glabrous; I have seen two gatherings with hairs on the indusia but they were otherwise indistinguishable from plants with glabrous indusia. The segments of the fertile pinnae are narrow, and the sterile pinnae do not differ much from the fertile ones except that the pinna segments tend to be less narrow and the lobing less deep, sometimes to little more than half way to the costa, though they are still strongly forwardly-directed.

Ching did not question Ceylon and Javan plants as being conspecific. Holttum (in *Reinwardtia, loc. cit.*) queried the occurrence of true *Trigonospora calcarata* in Ceylon on the grounds that plants from there, though similar to Javan specimens, were considerably larger. Javan specimens are very uniform. Blume's type has one frond 35 cm long with pinnae 2–3 cm long but of the 14 Javan sheets examined, most have shorter fronds and all have pinnae 2–3 cm long with 4 cm as the longest. Specimens from Ceylon are mostly both

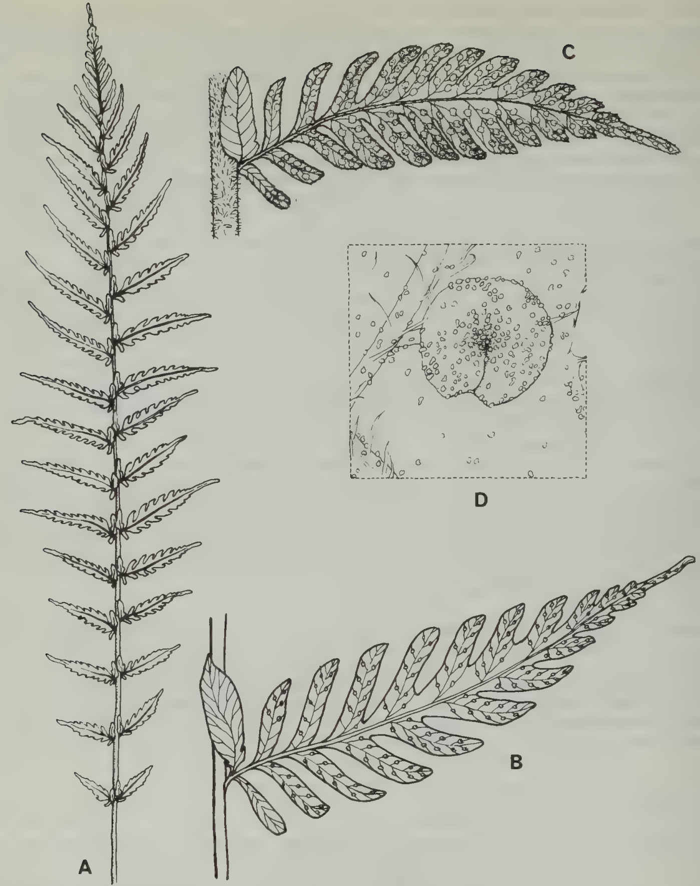

Fig. 4 A–*Trigonospora angustifrons* Sledge, frond (*Sledge* 1246, holotype), × 0·5; B–*T. calcarata* (Blume) Holttum, pinna (Sledge 1042), × 2; C–*T. glandulosa* Sledge, pinna (*Sledge* 808, holotype), × 2; D–part of under surface of C, showing subsessile glands on lamina surface and indusium, × 30.

considerably larger and more variable. The average length of the pinnae is twice that of Javan plants. Though such plants appear to be different they display all the essential characters which distinguish *T. calcarata* from other species of *Trigonospora* without having any additional distinctions, and since some gatherings from Ceylon are scarcely distinguishable in size, as well as in frond architecture, from Javan plants, I believe all should be included within *T. calcarata.*

Thwaites was probably influenced by Hooker when he included all Trigonosporas within the one species, *Aspidium calcaratum*, for he was evidently aware of the difference between *Trigonospora calcarata s.str.* and *T. caudipinna* since, of the two Thwaites C.P. numbers quoted in his *Enumeratio*, specimens sent out as C.P. 1363 were nearly all *T. caudipinna*, whilst C.P. 3273 was nearly all *T. calcarata*. Gardner's two numbered but unnamed collections were similarly not mixtures of two species; his no. 1107 was invariably *T. caudipinna*, whilst no. 1250 was consistently *T. calcarata*.

5. **Trigonospora angustifrons** Sledge, **sp. nov.** (Fig. 4A)

Caudex erectus. Frondes 20–40 (45) cm longae, stipites breves, fertiles quam steriles vix longiores. Stipes rhachisque glabra praeter in sulco dorsali rhachidis pubescentes. *Lamina linearis-oblonga* 5–6 cm lata, *triplo ad sexies longior* cum fere 15 jugis pinnarum liberarum ascendentium, infima juga non deflexa. Pinnae fusiformis usque ad 4 cm longae 5–8 mm latae, cum octo vel paucioribus jugis segmentorum obliquorum falcatorum, fere ad dimidium costae (raro ultra) incisae in parte medio latissimo, *basin versus attenuatae paribus infimis segmentorum omnino liberis, erectis,* acroscopicis saepe leviter lobatis et rhachidi postice applicatis; pinnae distales serratae vel crenatae supremae integrae; apices pinnarum acuminati integri; *paginae supra et infra omnino glabrae,* margines non ciliati. Indusia glabra.

Caudex erect. Fronds 20–40 (45) cm long, stipes short, the fertile ones not much longer than those of the sterile fronds. Stipe and rhachis glabrous beneath, hairy in the dorsal groove of the rhachis. *Lamina linear-oblong,* 5–6 cm wide and *3–6 times as long,* with about 15 pairs of free ascending pinnae, the lowest pair not deflexed. Pinnae fusiform, up to 4 cm long, 5–8 mm wide with 8 pairs or fewer of oblique falcate segments, cut half way (rarely more) to the costa in the broadest middle region, *narrowed at the base with the lowest pair of segments quite free,* the acroscopic segment often slightly lobed and closely applied to the rhachis; distal pinnae serrate or crenate, the uppermost entire; apex of pinnae acuminate, entire; *surfaces quite glabrous above and beneath* or with a few hairs on the costa above; margins not ciliate. Indusia glabrous.

Collections: At foot of Adam's Peak near Carney, Ratnapura District, by river, 240 m, 9 March 1954, *Sledge* 1246 (BM, holotype). Near Rassagala east of Ratnapura, edge of river in forest, 750 m, 16 Nov. 1976, *Faden* 76/316 (K). Adam's Peak, *Moon* (BM). Unlocalised: *F.D'A Vincent* (CGE).

By streams and rivers at low to medium altitudes about Adam's Peak.
Endemic to Ceylon.

A well-marked species related to *Trigonospora calcarata,* but distinguished by its narrow fronds, often six times as long as broad, and by the whole plant, save the dorsal groove of the stipe and rhachis, being quite glabrous. The pinnae resemble those of *T. zeylanica* in size and their fusiform outline with strongly cuneate bases, but in *T. angustifrons* a pair of free, erect basal segments adjacent to the rhachis is always present. The next pair of segments appear to be somewhat distant from the basal pair on account of their being very oblique to the pinna axis with cuneate hinder margins.

Apparently a rare species; the three localised gatherings all come from the Peak Wilderness area.

6. **Trigonospora glandulosa** Sledge, **sp. nov.** (Fig. 4 C, D)

Caudex erectus. Frondes usque ad 40 cm longae, fertiles stipitibus quam steriles longioribus non prominenter, *stipes rhachisque omnino cinerei-tomentosi* cum pilis brevibus crispatis et (praesertim in rhachidi) pilis longioribus patulis acicularibus 1 mm longis vestitis. Lamina 15–30 × 6–8 cm in ambitu anguste oblonga vel elliptica sursum angustata, fere 10–12 interdum usque ad 16 juga pinnarum liberarum infimis non deflexas. Pinnae 3–5 × 0·5–

1·0 cm profunde pinnatifidae usque ad 10 paria segmentorum obliquorum oblongorum obtusorum falcatorum 2 mm latorum, *segmenta infima omnino libera,* interdum breviter petiolata saepe prope basin lobata leniter ampliata contigua et saepe subter rhachin disposita; aliquando jugum secundum segmentorum similiter ad basin liberum, residuum pinnae paulatim minus profunde partitum in segmentis obliquis obtusis falcatis; pinnae ad apicem obtusae vel acutae pinnae supremae et illae ad partem apicis adnatae omnino integrae. Costae costulaeque utrinque pilis acicularibus instructae et margines segmentorum pilis potius rigidis fimbriatae: *pagina infera glandibus copiosis subsessilibus flavescentibus*; pagina superna in juventute glandibus similiter glabrescens; *indusium latum tenue glandibus obtectum* cum vel sine pilis setosis intermixtis.

Caudex erect. Fronds up to 40 cm long the fertile ones with stipes not conspicuously longer than those of the sterile fronds, both *stipe and rhachis densely grey-pubescent throughout* with a mixture of short crisped hairs and some longer, spreading acicular hairs 1 mm long. Lamina 15–30 × 6–8 cm narrowly oblong or elliptic in outline, tapering above, with about 10–12, less commonly up to 16 pairs of free pinnae, the lowest pair not deflexed. Pinnae 3–5 × 0·5–1 cm, deeply pinnatifid with up to 10 pairs of oblique, oblong blunt falcate segments 2 mm wide, *the basal pair quite free* and sometimes shortly stalked, often lobed near the base slightly enlarged and lying close to or often underlying the rhachis, sometimes the second pair of segments also free to the base, the rest of the pinna becoming progressively less deeply cut into oblique, blunt, falcate lobes; apex of pinnae blunt or acute, uppermost pinnae and those adnate to the apical portion becoming quite entire. Costas and costules with scattered acicular hairs above and below and the margins of the segments fringed with rather stiff hairs, *under surface with copious, subsessile, pale, yellow glands,* upper surface with similar glands when young, becoming smooth with age; *indusium broad, thin, covered with glands* and with or without intermixed setose hairs.

Eight miles north-east of Ratnapura, in rocky ground by stream in shady ravine, 150 m, 4 Jan. 1951, *Sledge* 808 (BM, holotype; US). Same locality and date, *Ballard* 1383 (K).

Shady bank by stream at low elevation near Ratnapura.
Endemic to Ceylon.

The new species differs from all other known taxa of *Trigonospora* in the glandular clothing of the pinnae and indusia. The glands have very short stalks and spherical heads. The densely felted stipe and rhachis are also distinctive. The lowermost pair of pinna segments is quite free as in *T. calcarata* and *T. angustifrons* and the second acroscopic segments are also sometimes free to the base.

Fronds which have not been submerged in water are easy to recognise by the copious, pale-yellow glands, especially on the under surfaces and indusia. In fronds which have been inundated however, easily distinguished by the quantities of grit and other debris lodged in the hairy coating of the stipe and rhachis, the glands seem to be absent, suggesting that they are easily detached and washed off the leaf surfaces.

This is the plant referred to as '*Thelypteris* n.sp.' in Manton & Sledge (*Phil. Trans. R. Soc. Lond.* B, **238:** 137 (1954). It was examined cytologically and found to be a diploid with n = 36. Only known from the type locality where it was abundant and uniform.

7. **Trigonospora zeylanica** (Ching) Sledge, **comb. nov.** (Fig. 2C)

Thelypteris zeylanica Ching in *Bull. Fan meml Inst. Biol.* (Bot.) **6** : 287 (1936). Type: Ceylon, *Thwaites* C.P. 3050 (K).

Nephrodium (Lastrea) falcilobum var. *β* Hook., *Sp. Fil.* **4** : 108 (1862). Type: Ceylon, *Thwaites* C.P. 3050 (K).

Lastrea calcarata Bedd., *Ferns S. Ind.* : 82, t.246 (1864), *nom. illeg.*, non *L. calcarata* (Blume) Moore (1858). Type: Ceylon, *Thwaites* C.P. 3050 (K).

Aspidium calcaratum var. *β* Thwaites, *Enum, Pl. Zeyl.*: 391 (1864). Bedd., *Handb. Ferns Brit. Ind.* : 237 (1883).

Lastrea calcarata var. *moonii* Trimen in *Syst. Cat. Fl. Pl. Ferns Ceylon* ex *Journ. Ceylon Branch Roy. Asiat. Soc.* : 114 (1885), *nom. nud.—Dryopteris calcarata* var. *moonii* Trimen in Willis, *Rev. Cat. Fl. Pl. Ferns Ceylon, Peradeniya Manuals* **2** : 116 (1911), *nom. nud.*

Caudex erect, fronds up to 40 cm long, the fertile ones with stipes not much longer than those of the sterile fronds. Lamina 15–30 cm long usually 3–6 cm wide but sometimes up to 9 cm, narrowly oblong to elliptic oblong in outline with about 15 pairs of free pinnae, the lowermost pair not deflexed. Pinnae linear-oblong to oval-oblong or fusiform, 2–5 cm long, 4–10 mm wide rarely cut half way to the costa into about 8 pairs of oblique falcate lobes, often the margins little more than serrate, the distal pinnae entire or subentire; *base of pinnae narrowly cuneate* and often shortly stalked at least in the lower pinnae, with *no basal pinna segments adjacent to the rhachis*; apex of pinnae blunt. Rhachis and upper surface of costa hairy and margins of segments sometimes with scattered hairs, otherwise surfaces glabrous above and below. Indusia glabrous.

Collections: Thwaites C.P. 3050 (BM; CGE; K; P; PDA: Hinidoon, Dec. 1853; Singh Rajah Forest, April 1855). *Thwaites* C.P. 992 (BM; CGE; K; P, partim; PDA: Saffragam, Aug. 1821, *Moon*). Above Enselwatte Estate above Deniyaya, shaded places by rivulet, June 1969, *Kostermans* 23658 (US). Kanneliya Forest near Hiniduma, low alt., 7 May 1973, *Kostermans* 24736 (US). Same locality, 7 Dec. 1976, *Faden* 76/504 (K). Sinha Raja Forest near Hedigala, stream side, 75 m, 5 Jan. 1951, *Sledge* 812 (BM). Pahale Hewissa, by stream, 30 m, 31 March 1954, *Sledge* 1370 (BM; K; US). Same locality, 20 Jan. 1951, *Ballard* 1522 (K).

By streams in forest at low elevations in the south of the island.

Endemic to Ceylon.

A very distinct species easily recognised by its shallow-lobed or merely serrate pinnae with strongly cuneate bases. The pinnae are often shortly stalked but this is not always the case. They are, however, always devoid of basal segments lying close to the rhachis; all other Ceylonese species of *Trigonospora* have these basal segments.

A sheet at Peradeniya, without collector's name or date, purporting to have come from Hakgala, is almost certainly wrongly localised; all other gatherings are from low elevations in the southern part of Ceylon.

X. PSEUDOCYCLOSORUS Ching

in *Acta phytotax. sin.* **8** : 322 (1963), emend, Holttum in *Jl S. Afr. Bot.* **40** : 137 (1974).

Caudex erect or short-creeping; fronds bipinnatifid with abrupt transition at the base to numerous small pinnae and often reduced to swollen tubercles; aerophores present at base of lower and reduced pinnae; upper surfaces of costae grooved; veins free, usually raised below, the acroscopic basal one passing to the base of the sinus between adjacent pinna segments, the basiscopic one reaching the edge above the base of the sinus or the two veins converging but not fusing at the sinus base; surfaces glabrous or with acicular hairs, eglandular; sori indusiate, sporangia without hairs or glands but usually with a septate hair on the stalk. n = 36 (35 also reported).

About 12 species; three in Africa and nine in tropical and subtropical Asia to Japan and Luzon.

1. **Pseudocyclosorus tylodes** (Kunze) Ching

in *Acta phytotax. sin.* **8** : 323 (1936) [as '*xylodes*'.]—*Aspidium tylodes* Kunze in *Linnaea* **24** : 244, 283 (1851) ['*xylodes*' *loc. cit.* : 281]; Thwaites, *Enum. Pl. Zeyl.* : 391 (1864). Type: India, Nilgiris, *Schmid* (B).—*Lastrea tylodes* (Kunze) Moore, *Index Fil.* : 107 (1858). Copel., *Fern Fl. Philipp.* : 330 (1960) [as '*xylodes*.']—*Lastrea ochthodes* var. *tylodes* (Kunze) Bedd., *Ferns S. Ind.* : t.107 (1863); *Handb.*

Ferns Brit. Ind. : 240 (1883).—*Nephrodium prolixum* var. *tylodes* (Kunze) Baker, in Hook.& Baker, *Syn. Fil.* : 268 (1867).—*Dryopteris tylodes* (Kunze) Christensen, *Not. Syst.* **1** : 41 (1909) [as '*xylodes*']; *Index Fil., suppl.* **3** : 102 (1934), [as '*xylodes.*']—*Thelypteris tylodes* (Kunze) Ching in *Bull. Fan meml Inst. Biol.* (Bot.) **6** : 296 (1935) [as '*xylodes.*']

Caudex erect, fronds tufted; stipes up to 50 cm long bearing ovate, brown scales near the base, elsewhere glabrous; lamina commonly 40–60 cm long and 10–20 cm wide, sometimes 100 cm long, oblong-lanceolate in outline, pinnate with 20–30 pairs of sessile narowly lanceolate pinnae, in large fronds the pinnae up to 30 × 2·5 cm, in small fronds less than half this size, apex of pinnae acuminate, base bearing a dark-coloured aerophore on the underside, *margins cut down ¾ of the way to the costa* into falcate, acute segments with revolute margins, *veins* about 10 pairs per segment, *prominent on both surfaces,* the *lowermost pair connivent but not confluent at the base of the sinus*; lowermost pinnae not or little shortened but *several pairs of abortive pinnae represented by tubercle-like vestiges distributed along the stipe*; rhachis hairy above, glabrous beneath; *pinnae glabrous on both sides* save for the costae which are strigose hairy above; texture stiff, subcoriaceous; sori inframedial, indusium firm, glabrous persistent. Spores verrucose.

Collections: Thwaites C.P. 1361 (BM; CGE; K; P; PDA). Newera Eliya, shady woods, Sept. 1844, *Gardner* 1108 (CGE; K). Newera Eliya, 22 Jan. 1908, *Bicknell* (P). Rambodde, *Beckett* (BM). Hakgala, stream banks in jungle, 28 Feb. 1906, *J. C. Willis* (PDA). Corbets Gap, by track through jungle, 1200–1300 m, 9 Dec. 1950, *Sledge* 551, 571 (BM). Ramboda, bank by roadside, 1575 m, 17 Dec. 1950, *Sledge* 659 (BM). Between Pattipola and Horton Plains, by stream in jungle, 1950 m, 20 Dec. 1950, *Sledge* 669 (BM). Horton Plains, by stream in jungle, 2000 m, 19 Dec. 1950, *Sledge* 688 (BM). Riverstone Estate, Matale District, Central Province, 1100 m, 19 Jan. 1977, *Faden* 77/183 (K). Unlocalised: *Freeman* 236, 237 (BM). *Robinson* 160 (K). *Walker* (K; P).

In mountain forests of the Central Province above 1000 m.
Southern India and Ceylon.

Very large plants may have pinnae 30 cm long but 10–15 cm is a normal size. A small form is occasionally met with in which the whole frond scarcely exceeds 30 cm and the pinnae are then 4–6 cm long. My specimens (no. 551, 571) from Corbets Gap are such forms and are very closely matched by *Gamble* 12122 and 15317 (K) from the Nilgiris and by two sheets from Ceylon at Paris. These small forms bear a superficial resemblance to *Trigonospora ciliata* and have sometimes been misidentified as that species, although the presence of abortive pinnae on the stipes and the prominent raised veins are sufficient to distinguish them.

Holttum (in *Br. Fern Gaz.* **11** : 55–56 (1974)) has discussed the alternative spellings *xylodes* and *tylodes* and shown that the latter epithet (which has a descriptive significance lacking in the former) is the spelling which Kunze almost certainly intended.

Pseudocyclosorus ochthodes (Kunze) Holttum is not a Ceylonese fern. It was recorded from Ceylon in Beddome's *Handbook* because Thwaites misconstrued Kunze's *Aspidium ochthodes,* the species referred to under that name in *Enum. Pl. Zeyl.* : 392 (1864) being *Amphineuron opulentum* (*Nephrodium extensum* (Blume) Moore). Though this error was subsequently corrected and the record withdrawn in *Handb. Suppl.* : 54 (1893), the emendation has been overlooked by some later writers.

XI. AMPHINEURON Holttum

in *Blumea* **19** : 45 (1971).

Caudex erect, decumbent or long-creeping; fronds bipinnatifid the basal pinnae narrowed at their bases, not reduced in size; basal veins either free or anastomosing to form a short excurrent vein to the base of the sinus between adjacent pinna segments, the rest free; lower surface of pinnae bearing short acicular hairs and commonly also subsessile, often yellow glands; sori usually confined to lobes of pinnae, usually indusiate; indusia often glandular, sporangium not bearing hairs or glands near the annulus, stalks commonly bearing a short, gland-tipped hair; spores dark, irregularly tuberculate or with irregular thick, branched ridges. $n = 36$.

About 12–15 species; one widespread in Africa, Mascarene Islands and south-east Asia to Australia (northern Queensland) and the Pacific Islands, the rest mainly in south-east Asia, Malesia and Melanesia.

1. **Amphineuron opulentum** (Kaulf.) Holttum

in *Blumea* **19** : 45 (1971).—*Aspidium opulentum* Kaulf., *Enum. Fil. Chamisso* : 238 (1824). Type: Guam, *Chamisso* (LE).

Aspidium extensum Blume, *Enum. Pl. Jav.* : 156 (1828). Type: Java, Pulo Pinang, *Blume* (L).—*Nephrodium extensum* (Blume) Moore, *Index Fil.* : 91 (1858). Bedd., *Handb. Ferns Brit. India* : 269 (1883).—*Dryopteris extensa* (Blume) Kuntze, *Rev. Gen. Pl.* **2** : 812 (1891).—*Cyclosorus extensus* (Blume) Ching in *Bull. Fan meml. Inst. Biol.* (Bot.) **8** : 182 (1938). Holttum, *Rev. Fl. Malaya* **2** : 264, fig. 150 (1955).—*Thelypteris extensa* (Blume) Morton, *Am. Fern J.* **49** : 113 (1959). Schelpe, *Fl. Zamb. Pterid.* : 193 (1970).

Nephrodium punctatum Parish ex Bedd., *Ferns Brit. India* : t.131 (1866). Type: Burma, Moulmein, *Parish* (K).

Aspidium ochthodes sensu Thwaites, *Enum. Pl. Zeyl.* : 392 (1864).

Rhizome creeping; stipes up to 60 cm sometimes longer, clothed near the base with linear brown scales, elsewhere minutely hairy; lamina bipinnatifid up to 90 cm long with 15–25 pairs of pinnae, the lowest pair sometimes much reduced in size; pinnae up to 35 × 3 cm in large fronds, half this size in small ones, apex acuminate, base obliquely truncate in the upper pinnae becoming cuneate in the lowest pinnae, *margins lobed about $\frac{2}{3}$ down to the costa,* the lobes oblique, slightly falcate with acute apices, *margins not ciliate*; veins 10–12 pairs, the *lowest veins of adjacent groups sometimes anastomosing below the base of the sinus, sometimes meeting at the sinus-base* or *sometimes passing to the edges of the sinus just above the base*; upper surfaces of costae strigose-hairy, the costules with a few scattered hairs, the veins glabrous or almost so, lower surfaces minutely pubescent on the costae, the *veins bearing copious small yellow glands*; sori supramedial, impressed and forming pustules on the upper surface, normally confined to the lobes, the basal 3–5 pairs of veins being sterile but occasionally all veins fertile; *indusia with small glands on the margins,* the surfaces glabrous or with a few hairs.

Collections: Thwaites C.P. 975 (BM; CGE; K; P, in part; PDA). C.P. 990, *Trimen* in herb. Beddome (K). *Gardner* 1362 (K). *Gardner* 1106 (sic) (BM; CGE). Heights above Kandy, Nov. 1829, *Col. Walker* (K). Hewelkandura on Koslanda—Wellawaya road, Monaragalla Dist., Uva Province, *c.* 400 m, 26 Dec. 1976. *Faden* 76/593 (K). Kandy Catchment, in secondary jungle, 750 m., 4 Feb. 1954, *Sledge* 1094 (BM). Lady Horton's Walk, Kandy, in secondary jungle above river *c.* 600 m, 16 Feb. & 24 March 1954, *Sledge* 1142, 1354 (BM). Unlocalised: 1839, *Mackenzie* (K). *Geo. Wall* (K; PDA). *Ferguson* (PDA; US). *Robinson* 161 (K).

Widely distributed but not very frequent in forests at all altitudes up to 1250 m.

East Africa, Seychelles, southern India, Ceylon, Burma, Thailand, Malesia, Australia (northern Queensland), New Caledonia eastwards to Tahiti and Marquesas.

The small golden-yellow glands on the veins in both the Ceylonese species of *Amphineuron* are distinctive. In *A. opulentum* the veins are more plentifully supplied with such glands than are those of *A. terminans,* and the indusia are invariably studded with glands round their margins, a feature absent from *A. terminans.* The basal pair of veins of adjacent pinna-lobes may unite below the sinus or remain free from one another within the same pinna. As a rule only the tips of the pinna lobes bear sori in *A. terminans,* rarely more than five of the distal veins on the basiscopic side being fertile, with fewer or none on the acroscopic side. In *A. opulentum* at least seven of the distal veins on both sides of the costule are usually fertile, and sometimes all the veins carry sori.

2. **Amphineuron terminans** (Hook.) Holttum

in *Am. Fern. J.* **63** : 82 (1973).—*Nephrodium terminans* Hook., *Spec. Fil.* **4** : 73 (1862). Bedd., *Ferns S. India* : t.90 (1863). Type: Kumaun, *Wallich* 386 in Herb. Hook. (K).

Nephrodium pteroides sensu J.Sm., *Cat. Cult. Ferns* : 54 (1857). Baker, *Syn. Fil.* : 289 (1868) *p.p.* Bedd., *Handb. Ferns Brit. India* : 296 (1883), non *Polypodium pteroides* Retz.—*Dryopteris pteroides* sensu Christensen, *Ind. Fil.* : 287 (1905) p.p., non *Polypodium pteroides* Retz.

Dryopteris interrupta sensu Ching in *Lingnan Sci. J.* **12** : 566 (1933), non *Pteris interrupta* Willd.—*Cyclosorus interruptus* sensu Ching in *Bull. Fan meml. Inst. Biol.* (Bot.) **8** : 184 (1938) Holttum, *Rev. Fl. Malaya* **2** : 262, fig. 149 (1955), non *Pteris interrupta* Willd.

Rhizome wide-creeping; stipes 60 cm or more long, scaly at the base, hairy in the groove, becoming glabrescent, rhachis hairy above; lamina up to 90 cm long with up to 25 pairs of free pinnae beneath the pinna-like apex, the lowest pair (or two) often reduced to small auricles; largest pinnae up to 35 × 2·5 cm but often only half this size, apex long-acuminate, base obliquely truncate in upper pinnae becoming attenuate in lower ones, *margins lobed from ¼ up to ½ way to the costa,* the lobes usually broadly rounded to subtruncate above with forward-pointing tips or sometimes obliquely triangular and falcate, the *margins fringed with setose hairs*; veins 6–12 pairs, *the basal pair anastomosing and forming an excurrent vein to the base of the sinus,* the next pair passing to the sinus membrane; upper surface of costae strigose-hairy, the costules and veins with scattered setose hairs at least in the lobes, lower surface minutely pubescent on the costae, costules and veins with small *yellow glands on the veins especially in the distal parts of the lobes; sori* supramedial on the upper veins *always confined to the lobes and often to the terminal parts of the lobes; indusia* broad, thin, surfaces usually with a few hairs, *margins eglandular.*

Collections: Thwaites C.P. 990 (BM; CGE; P; PDA). Hantane Range, in forests, July 1844, *Gardner* 1106 (CGE; K; P). Common at Kandy, *Mrs Chevalier* (BM). Heneratgoda, in jungle, 13 July 1927, *J. M. de Silva* (PDA). Rawana ella Falls, Ella–Wellawaya road, Ella Pass, Badulla Dist., Uva Province, *c.* 775 m, 18 Nov. 1976, *Faden* 76/371 (K). Lady Horton's Walk, Kandy, *c.* 600 m., 11 Dec. 1950, *Sledge* 582 (BM). Kadugannawa, amongst undergrowth below *Hevea* trees near roadside *c.* 300 m, 12 Dec. 1950, *Sledge* 584 (BM). Hunnasgiriya, *c.* 870 m, 16 Jan. 1954, *Sledge* 965 (BM). Ravine south of Bibile, Uva Province, 450 m, 22 Feb. 1954, *Sledge* 1172 (BM). Unlocalised: *Robinson* C151 (K). *Bradford* ex herb. *Hance* (BM). Randall in herb. *Rawson* 3220 (BM). *Ferguson* (PDA; US).

Widespread and not uncommon in forests in the west and centre.

Southern India and Burma to China (Hainan Dao); throughout Malesia to New Guinea and Australia (northern Queensland).

XII. CHRISTELLA H. Lév.

Fl. Kouy-tchéou : 472 (1915), emend. Holttum in *Taxon* **20** : 533 (1971) and *Blumea* **19** : 43 (1971).

Caudex erect to wide-creeping; fronds pinnate, decrescent with 1–5 pairs of lower pinnae gradually reduced, or rarely the lowest pinnae deflexed but not or scarcely reduced; pinnae pinnatifid, lobed or crenate; aerophores not conspicuous; veins anastomosing, rarely free, costas, costules, veins and lamina surface bearing erect, acicular hairs and sometimes small capitate hairs beneath and sometimes also thick, blunt, orange-coloured glands; sori indusiate, sporangia lacking setae or glands near the annulus but always bearing unicellular, elongate, glandular hairs on the stalks of the sporangia: spores with incomplete anastomosing wings or verrucose. n=36.

About 50 species, mainly in tropical and subtropical regions of Asia, with smaller numbers in Africa and America.

Holttum's account of *Christella* (in *Kew Bull.* **31** : 293–339 (1976)) is prefaced by a discussion of generic characters and of the systematic problems posed by variability and hybridisation in the genus. Few groups of ferns were less well understood by Beddome and his contemporaries. That variability is, in part, due to hybridisation now seems probable, for the readiness with which hybrids may be synthesised experimentally leaves scarcely any doubt that they must also occur in nature where different species grow intermixed. But the extent to which variation is genetically controlled or environmentally influenced is unknown, and cytotaxonomic and experimental studies are much needed for further progress in the understanding of this difficult genus. Both Manton and A. R. Smith have emphasised the occurrence of abortive spores as one of the best ways of recognising hybrid specimens. But it does not follow as a corollary that the formation of sound, or apparently sound, spores necessarily disproves hybrid origin, and the occurrence of mixed characters in some specimens seems irreconcilable with their being of pure stock.

The spores of *Christella* are of two types. In one the wall is raised into narrow irregularly anastomosing, short and incomplete wings. This type I refer to briefly as ridged. In the other type the wall forms more or less flattened, spine-like outgrowths with irregular apices, not joined to form interrupted wings. These two types are illustrated by Wood in *Bot. J. Linn. Soc.* **67** (Suppl. 1): 194, pl. 1 A and E (1973). The second type of spore ornamentation, here referred to as verrucose, is found in *C. papilio* and *C. meeboldii*; other Ceylonese species of *Christella* all have spores of the first type.

I have felt it unnecessary to repeat all the citations of synonyms given under each species in Holttum's work, especially where these are names originally given to gatherings from areas remote from Ceylon. My aim has been to include names given in works dealing with Ceylon, India and the western Malayan region. In some instances the references to Hooker's or Beddome's works, as cited in synonymy by Holttum, are differently construed by me.

Seven species are recognised in the following account. Two of the species credited to Ceylon by Holttum: *Christella malabariensis* and *C. taprobanica*, I reject for the reasons given in the discussions under *C. dentata* and *C. papilio*. Only two species, *C. parasitica* and *C. dentata* are common and widespread. The distribution of *C. hispidula* and *C. papilio* is not well known; they are infrequent but probably occur in many different stations where suitable conditions obtain. Two other species, *C. subpubescens* and *C. meeboldii* are at present known only from one and two gatherings respectively. Although both may have been overlooked through confusion with other species, it is more likely that the absence of specimens in all the collections examined gives a true indication of their rarity. The seventh species *C. zeylanica* has not been regathered during the present century.

Key to species of Christella

1	One or more pairs of lower pinnae distinctly shortened	2
–	Lowermost pair of pinnae not or hardly shortened, but often deflexed	1. **C. parasitica** (p. 29)
2(1)	Rhizome erect, fronds tufted	3
–	Rhizome creeping, fronds spaced	4
3(2)	One pair of veins anastomosing : pinnae hairy beneath	3. **C. hispidula** (p. 33)
–	1½–2 pairs of veins anastomosing : pinnae subglabrous beneath	6. **C. papilio** (p. 37)
4(2)	Pinnae subentire, crenate or very shallowly lobed	7.**C. zeylanica** (p. 39)
–	Pinnae pinnatifid	5
5(4)	Up to 4 pairs of basal pinnae shortened	6
–	Five or more pairs of basal pinnae shortened	6. **C. papilio** var. **repens** (p. 37)
6(5)	At least some pinnae with 2 pairs of veins fusing below the sinus membrane; pinnae lobed less than half way to costa	7
–	1–1½ pairs of veins fusing below the sinus membrane; pinnae lobed about half way to costa	2. **C. dentata** (p. 32)
7(6)	Pinnae glabrous or nearly so beneath except on costa	4. **C. subpubescens** (p. 35)
–	Pinnae hairy beneath	5. **C. meeboldii** (p. 36)

1. **Christella parasitica** (L.) H. Lév. (Fig. 5A)

Fl. Kouy-Tchéou: 475 (1915).—*Polypodium parasiticum* L., *Sp. Pl.* : 1090 (1753). Type: Canton, *Osbeck* (S—PA, in herb. Swartz).—*Nephrodium parasiticum* (L.) Desvaux in *Mém. Soc. linn. Paris*

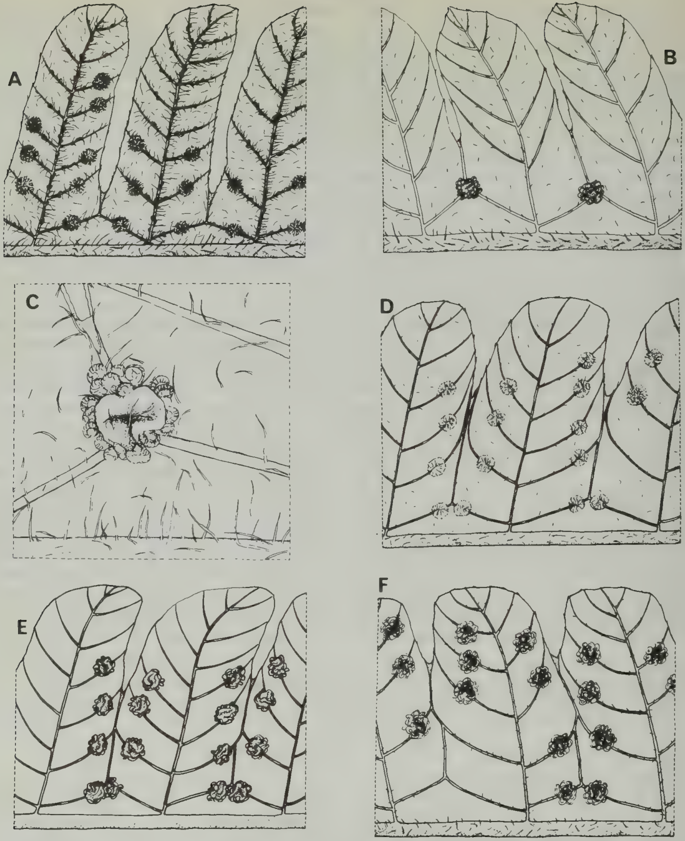

Fig. 5 Pinna segments: A–*Christella parasitica* (L.) H. Lév. (*Sledge* 844), × 5; B–*C. hispidula* (Decaisne) Holttum (*Sledge* 578), × 5; C–portion of B enlarged to show sorus and hairs, × 20; D–*C. dentata* (Forssk.) Brownsey & Jermy (*Sledge* 924), × 5; E–*C. subpubescens* (Blume) Holttum (*Sledge* 585), × 5; F–*C. meeboldii* (Rosenst.) Holttum (*Meebold* 2133), × 6.

6 : 260 (1827). C. B. Clarke in *Trans. Linn. Soc.* (Bot.) II. **1** : 533 (1880) p.p.—*Dryopteris parasitica* (L.) Kuntze, *Rev. Gen. Pl.* **2** : 811 (1891). Christensen in *Ark. Bot.* **9**(11) : 26, fig. 4 (1910); in *Gard. Bull. Str. Settl.* **4** : 389 (1929).—*Cyclosorus parasiticus* (L.) Farwell in *Amer. Midl. Nat.* **12** : 259 (1929). Ching in *Bull. Fan meml Inst. Biol.* (Bot.) **8** : 201 (1938). Holttum, *Rev. Fl. Mal.* **2** : 281, fig. 162 (1955).—*Thelypteris parasitica* (L.) Tardieu in *Notul. Syst.* **7** : 75 (1938). K. Iwats. in *Mem. Coll. Sci. Kyoto Univ.* B, **31** : 172 (1965).

Nephrodium molle Hook., Sp. Fil. **4** : 67 (1862) p.p.; Bedd., *Ferns S. Ind.*: t. 84 (1863); *Handb. Ferns Brit. Ind.* : 277 (1883) p.p. and *Handb. Suppl.* : 76 (1892) p.p., non *A. molle* Swartz. —*Aspidium molle* sensu Thwaites, *Enum. Pl. Zeyl.* : 391 (1864) p.p., non Swartz (1801).

Aspidium procurrens Mettenius in *Annls Mus. Bot. Lug.-Bat.* **1** : 231 (1864). Type: Java, *Zippelius* (L: 908, 335–152).—*Nephrodium procurrens* (Mettenius) Baker, *Syn. Fil.* : 290 (1867). C. B. Clarke in *Trans. Linn. Soc.* (Bot.) II. **1** : 530 (1880). Bedd., *Handb. Ferns Brit. Ind.* : 278 (1883); *Handb. Suppl.* : 67 (1892) p.p.—*Dryopteris procurrens* (Mettenius) Kuntze, *Rev. Gen. Pl.* **2** : 813 (1891). van Rosenb., *Malay. Ferns* : 211 (1908) p.p.—*Cyclosorus procurrens* (Mettenius) Copel., *Fern Fl. Philipp.*: 340 (1960) *nomen tantum.*—*Thelypteris procurrens* (Mettenius) C. F. Reed in *Phytologia* 17 : 306 (1968).

Nephrodium didymosorum Parish ex Bedd., *Ferns Brit. Ind.*, t.200 (1866). Type: Burma, Moulmein, *Parish* (not found in Herb. Kew).—*Nephrodium molle* var. *didymosorum* (Parish ex Bedd.) Bedd., *Handb. Ferns Brit. Ind.* : 279 (1883).—*Dryopteris didymosora* (Parish ex Bedd.) Christensen, *Index Fil.* : 262 (1905). van Rosenb., *Malay. Ferns* : 225 (1908) p.p.; *idem Suppl.* : 183 (1917).—*Cyclosorus didymosorus* (Parish ex Bedd.) Nayar & Kaur, *Companion Beddome* : 68 (1974).

Nephrodium tectum Bedd., *Handb. Suppl.* : 79 (1892), excl. *King* spec. Type: Singapore, *Wallich* 394 (K; W).

Rhizome creeping; stipes scaly at the base elsewhere more or less hairy according to age, up to 40 cm long; rhachis clothed throughout with soft, acicular, unicellular hairs. Lamina about as long as stipe or longer, pinnate with up to 20 pairs of pinnae and sometimes more; *basal pinnae deflexed, not or only slightly reduced.* Pinnae 7–15 × 1–2 cm, base truncate, apex acuminate, *lobed* $\frac{2}{3}$–$\frac{3}{4}$ *to costa,* veins 8–10 pairs in the lobes, the *lowermost veins* of adjacent lobes *joining to form an excurrent vein* to the sinus, the *next pair meeting the edge above the base of the sinus* or occasionally the second acroscopic vein terminating at the base of the sinus; basal acroscopic lobes of lower pinnae somewhat enlarged and normally incurved and repand; *lower surface* of pinnae covered *with soft spreading, acicular hairs* up to 1 mm long, and *thick orange or yellow glands normally present on the veins in the lobes; upper surface* of costae densely hairy, fewer hairs on the veins, surface of lamina between the veins *with* scattered short hairs and *subsessile colourless, gland-like capitate hairs.* Sori medial or slightly nearer the margin, rarely more than four pairs of veins in a lobe fertile and often only the lowermost veins bearing sori; indusia bearing long hairs. n = 72 tetraploid.

Collections: Thwaites C.P. 974 (BM, in part; CGE, in part; K; P, in part; PDA, in part). Peradeniya, 7 Feb. 1914, *Petch* (PDA). Roseneath, Kandy, edge of path in secondary jungle, 660 m, 28 Nov. 1950, *Ballard* 1000 (K). Kandy, 720 m, 9 April 1954, *Sledge* 1412 (BM). Corbets Gap, 1200 m, 7 Jan. 1951, *Sledge* 844 (BM). Nawanagalla, bushy ground by road through jungle, 1110 m, 8 Jan. 1954, *Sledge* 942 (BM). Jungle at Hunnasgiriya, 870 m, 16 Jan. 1954, *Sledge* 977 (BM). Panilkande, 600 m, 5 April 1954, *Sledge* 1401 (BM). Galaha, 940 m, 22 Jan. 1954, *Schmid* 1041 (BM). Badulla road from Nuwara Eliya, 29 Dec. 1950, *Ballard* 1313 (K). Bambaragalla, Matale District, 750 m, 12 Dec. 1976, *Faden* 76/530 (K). Unlocalised: *Mrs Chevalier* (BM). *Freeman* 270C, 271D, 272E, 273F (BM). *Barkly* (BM). *Alston* 1093 (K).

Very common in the Western, Central and Southern Provinces. At all elevations up to 1800 m, in open or lightly shaded, grassy or bushy places, and roadside banks.

India, Ceylon, south China and south Japan, through south-eastern Asia to Taiwan, New Caledonia and Australia (Queensland) and east to Polynesia.

Christella parasitica is distinguished from all other Ceylonese species of *Christella* by its non-decrescent fronds, the pinnae of which normally, though not invariably, have orange-coloured glands on the lower surface of the veins. Beddome and his contemporaries failed to distinguish the species and nearly all the descriptions of taxa in this group in Beddome's *Handbook* are compounded of two or more species, though his description of *Nephrodium molle* var. *didymosorum* refers exclusively to *Christella parasitica.* In the *Supplement* to his *Handbook* the description of *Nephrodium molle* includes three species. The first three lines refer to *Christella parasitica,* the next two lines are applicable to *C. dentata*, and the inclusion of *C. hispidula* is evidenced by the reference to erect rhizomes. His description of *Nephrodium tectum* is also compounded of *Christella parasitica* and *C. hispidula.* In the *Handbook* a fourth species is probably included in the description of *Nephrodium molle,* for two pairs of anastomosing veins and a glabrous indusium are the usual characters of *Christella subpubescens,* but not of the other three species which the description covers.

Nephrodium procurrens Baker is construed by Beddome as *Christella parasitica,* though his reference to 'the very large form . . . with the lower pinnae reduced to deltoid auricles' clearly refers to the fern which Hope later described as *Nephrodium papilio.* The latter is transferred in the *Supplement* to *N. molle* var. *major,* but *N. procurrens* remains a hybrid description covering *Christella parasitica* and *C. cylindrothrix.*

2. **Christella dentata** (Forssk.) Brownsey & Jermy (Fig. 5D)

in *Brit. Fern. Gaz.* **10** : 338 (1973). Holttum, in Jl S. Afr. Bot. **40** : 143 (1974).—*Polypodium dentatum* Forsskal, *Fl. Aegypt. Arab.* : 185 (1775). Type: Arabia, *Forsskal* (C).—*Dryopteris dentata* (Forsskal) Christensen in *K. dansk. Vidensk. Selsk. Skr.* VIII, **6**(1) : 24 (1920); *Index Fil. Suppl.* **3** : 84 (1934). Backer & Posth., *Varenfl. Java* : 58 (1939).—*Thelypteris dentata* (Forsskal) E. St. John in *Am. Fern J.* **26** : 44 (1936). Schelpe, *Fl. Zamb. Pterid.* : 197 (1970). A. R. Sm., *Univ. Calif. Publ. Bot.* **59** : 57 (1971).—*Cyclosorus dentatus* (Forsskal) Ching in *Bull. Fan meml Inst. Biol.* (Bot.) **8** : 206 (1938).

Polypodium nymphale G. Forster, *Fl. Ins. Austr. Prodr.* : 81 (1785). Type: New Zealand, *G. Forster* (BM).

Aspidium molle Swartz in *J. Bot. Göttingen* **1800** (2): 34 (1801) [nom. nov. pro *Polypodium molle* Jacq., *Collect. Bot.* **3** : 188 (1789), non Schreber (1771) nec All. (1785)] Type: cult. Vienna (W).—*Nephrodium molle* (Swartz) R.Br., *Prodr. Fl. N. Holl.* : 149 (1810). Hooker, *Sp. Fil.* **4** : 67 (1862), p.p. Bedd., *Handb. Ferns Brit. Ind.* : 277 (1883) p.p.; *Handb. Suppl.*: 76 (1892) p.p.—*Dryopteris mollis* (Swartz) Hieron. in *Hedwigia* **46** : 348 (1907). van Rosenb., *Handb. Suppl.*: 183 (1917), p.p.?

Nephrodium malabariense Fée, *Mém. Soc. Sci. nat. Strasbourg* **6** : 43 (1865). Type: Concan, *Law* ex herb. J. D. Hook. & Thomson (holotype not seen, BM lectotype).—*Thelypteris malabariensis* (Fée) Panigrahi in *Notes R. bot. Gdn Edinb.* **33** : 497 (1975).—*Christella malabariensis* (Fée) Holttum, in *Kew Bull.* **31** : 317 (1976) p.p.

Cyclosorus subpubescens sensu Holttum, *Rev. Fl. Mal.* **2** : 273, fig. 157 (1955), non *Aspidium subpubescens* Blume. Sensu Panigrahi & Manton in *J. Linn. Soc.* (Bot.) **55** : 729–743 (1958).

Cyclosorus jaculosus sensu Panigrahi & Manton *loc. cit.*, non *Aspidium jaculosum* Christ.

Thelypteris taprobanica Panigrahi in *Kew Bull.* **31** : 187 (1976) p.p., incl. holotype. Type: Ceylon, *G. Wall* (K).

Rhizome shortly creeping, fronds dimorphic, the fertile ones with more remote pinnae and standing high above the more spreading sterile fronds; stipes variable in length, scaly at the base elsewhere hairy as is the rhachis. Lamina longer than the stipe, pinnate with 15–25 pairs of free pinnae below the pinnatifid apex, *lower 1–4 pairs reduced* and widely spaced, the *basal acroscopic lobes of the lower pinnae enlarged,* often with lobed margins, its veins forked and sometimes anastomosing. Pinnae up to 14 × 1·5 cm, base truncate, apex acuminate, lobed about half way or a little more to the costa, veins 7–9 pairs in the lobes, the lowermost veins of adjacent lobes joining to form an excurrent vein to the sinus, the second acroscopic vein and sometimes the basiscopic vein also, reaching the excurrent vein at or about its confluence with the sinus membrane; *lower surface* of pinnae *eglandular,* normally pubescent *with short hairs on the veins and very short hairs on the lamina surface,* but sometimes almost glabrous, a few longer acicular hairs on the costa mixed with the prevailing shorter ones; *upper surface* of costae densely hairy, veins with short stiff hairs and some longer acicular hairs, lamina surface with or without short hairs, *subsessile capitate hairs absent.* Sori medial, four to six pairs of veins commonly fertile; indusia normally short-hairy, but sometimes glabrous. n = 72 tetraploid.

Collections: Thwaites C.P. 714 (BM; CGE; P). *Thwaites* C.P. 974 in part (BM; CGE; P; PDA). *Thwaites* C.P. 3498 (PDA, one of four sheets). Hantane Range, in forest, July 1844, *Gardner* 1105 (CGE). *Gardner* 1105 ex herb. J. Smith (BM). Lady Horton's Walk, Kandy, *Robinson* 148 (K). Hakgala, 1800 m, 23 Dec. 1950. *Sledge* 704 (BM). Hakgala Peak, *sub C. jaculosus,* Dec. 1950, *Manton* P199 (BM). Same locality, 1700–1800 m, 14 Nov. 1976, *Faden* 76/271 (K). Nuwara Eliya, *Freeman* 267A, 268A, 269B (BM). Jungle at Henaratgoda, 14 July 1927, *J. M. de Silva* (PDA). Kandy, in jungle, 3 June 1927, *Alston* 1093 (K; PDA). Corbets Gap, 1200 m, 7 Jan. 1951, *Sledge* 834 (BM). Two miles east of Panilkanda, edge of jungle near road, 660 m, 24 Jan. 1951, *Sledge* 924 (BM). Same locality & date. *Ballard* 1563 (K). Same locality, 5 April 1954, *Sledge* 1402 (BM). Hunnasgiriya, jungle 870 m, 16 Jan. 1954, *Sledge* 978 (BM). Le Vallon, forest, *c.* 1500 m, 9 Feb. 1954, *Sledge* 1128 (BM). Panadura, roadside in coconut plantation, 2–4 m, 14 Feb. 1968, *Comanor* 997 (K; PDA). Kadugannawa, on damp bank in rubber plantation, 12 Dec.

1950, *Ballard* 1091 (K). Bambragalla, Matale District, 750 m, 12 Dec., 1976, *Faden* 76/531 (K). Near Urugala, on Kandy-Mahiyangana road, 650 m, 24 Dec. 1976, *Faden* 76/562 (K). Bakinigahawela on Bibile-Moneragala road, shady stream bank, *c.* 250 m, 25 Dec. 1976, *Faden* 76/573 (K).

In similar situations to and as widespread as *Christella parasitica.*

Tropics and subtropics of Africa, Asia and Polynesia south to New Zealand. Introduced in America.

In the absence of rhizomes, the fronds of *Christella dentata* may be distinguished from those of *C. hispidula* by their venation. The second pair of veins in *C. hispidula* invariably reaches the margins of the lobes well above the base of the sinus (which lacks a distinct membrane), whereas in *C. dentata* one or both run into the sinus membrane and normally the second acroscopic vein fuses with the excurrent vein at or about the base of the sinus. The fronds also lack the small, colourless, gland-like, capitate hairs which occur on the upper surface of the pinnae in *C. hispidula.* They differ from *C. parasitica* in being dimorphic, decrescent and eglandular, the pinnae being short-hairy to subglabrous beneath and never with abundant long, soft, acicular hairs. *C. subpubescens* differs in its shallowly lobed, subglabrous pinnae in which two pairs of veins anastomose below the sinus.

Fée's description of *Nephrodium malabariense* includes no differences from *Christella dentata* other than minor quantitative distinctions, Holttum enlarged Fée's description to cover glandular plants, and both authors wrongly attributed the type locality to Malabar (see Sledge in *Kew Bull.* **34** : 78 (1979)).

The holotype of Panigrahi's *Thelypteris taprobanica* is a large, almost glabrous, form of *Christella dentata.*

3. **Christella hispidula** (Decaisne) Holttum (Fig. 5B, C)

in *Kew Bull.* **31** : 312 (1976).—*Aspidium hispidulum* Decaisne in *Nouv. Ann. Mus. Hist. nat. Paris* **3** : 346 (1834). Type: Timor, *Guichenot* (P).—*Nephrodium hispidulum* (Decaisne) Baker in Hook. & Baker, *Syn. Fil.* : 293 (1867) *nomen tantum—Dryopteris hispidula* (Decaisne) Kuntze, *Rev. Gen. Pl.* **2** : (1891). Christensen, *Index Fil.* : 271 (1905), excl. syn. *Nephrodium angustifolium* C. Presl, & *N. smithianum* C. Presl. van Rosenb., *Malay. Ferns* : 228 (1909), excl. syn. *N. angustifolium* C. Presl.—*Cyclosorus hispidulus* (Decaisne) Ching in *Bull. Fan meml Inst. Biol.* (Bot.) **10** : 245 (1941).—*Thelypteris hispidula* (Decaisne) C. F. Reed in *Phytologia* **17** : 283 (1968).

Nephrodium hilsenbergii C. Presl, *Epim. Bot.* : 47 (1851). Type: Mauritius, *Sieber* Syn. Fil. 49 (PRC, holotype; K, P, isotypes).—*Christella hilsenbergii* (C. Presl) Holttum in *Jl S. Afr. Bot.* **40** : 142 (1974).—*Thelypteris hilsenbergii* (C. Presl) Panigrahi in *Phytologia* **31 :** 369 (1975).

Nephrodium quadrangulare Fée, *Gen. Fil.* : 308 (1852). Type: Guyana, *Leprieur* 182 (?P, holotype; NY, isotype).— *Dryopteris quadrangularis* (Fée) Alston in *J. Bot. Lond.* **75** : 253 (1937).—*Cyclosorus quadrangularis* (Fée) Tardieu, *Phanérogamie* **14** : 345 (1952).—*Thelypteris quadrangularis* (Fée) Schelpe in *Jl S. Afr. Bot.* **30** : 196 (1964); **31** : 264, t.1 fig. b (1965); *Fl. Zamb. Pterid.* : 195 (1970). A.R.Sm., *Univ. Calif. Publs. Bot.* **59** : 64, fig. 114 (1971).

Nephrodium tectum Bedd., *Handb. Suppl.* : 79 (1892) p.p. quoad King spec. ex Perak.

Nephrodium molle sensu Bedd., *Handb. Ferns Brit. Ind.* : 277 (1883) p.p., *Handb. Suppl.* : 76 (1892) p.p., non *Aspidium molle* Swartz.

Dryopteris contigua Rosenst. in *Meded. Rijks.* **31** : 8 (1917). Christensen in *Gard. Bull. Str. Settl.* **7** : 244 (1934). Type: Borneo, *Teuscher* (L.).—*Cyclosorus contiguus* (Rosenst.) Ching in *Bull. Fan meml Inst. Biol.* (Bot.) **10** : 243 (1941). Holttum, *Rev. Fl. Mal.* **2** : 282, fig. 163 (1955).—*Thelypteris contigua* (Rosenst.) Reed in *Phytologia* **17** : 269 (1968).

Dryopteris repandula van Rosenb. in *Nova Guinea* **14** : 20 (1924). Type: western New Guinea, Mamberamo River, 90 m, *Lam* 1058 (BO, holotype; L, isotype)—*Cyclosorus repandulus* (van Rosenb.) Ching in *Bull. Fan meml Inst. Biol.* (Bot.) **10** : 248 (1941). Panigrahi & Manton in *J. Linn. Soc.* (Bot.) **55** : 729–743 (1958).—*Thelypteris repandula* (van Rosenb.) Reed in *Phytologia* **17** : 308 (1968).

Rhizome erect, fronds tufted; stipes usually short, 5 cm long, but sometimes 20 cm or more, stramineous, scaly at the base, elsewhere beset with pale, slender hairs; rhachis similarly clothed throughout with acicular hairs and densely so when young. *Lamina* (20) 30–60 (75) cm pale green or yellow-green in colour and softly herbaceous in texture, normally pinnate throughout with no terminal pinna-like part and with up to 30 pairs of pinnae; *decrescent below* with up to four pairs of pinnae shortened and deflexed and the basal acroscopic lobes of the middle and lower pinnae enlarged, incurved and more or less repand. Pinnae 7–15 × 1–2 cm, base truncate, apex acuminate, margins lobed $\frac{3}{4}$ to costa, veins 7–9 pairs in the lobes, *the lowermost veins* of adjacent lobes *joining to form an excurrent vein to the sinus* (which lacks a distinct basal membrane), *the next pair meeting the edge above the base of the sinus*; lower surface of pinnae with a mixture of acicular hairs 1–1·5 mm long and shorter hairs on the costae and mainly short hairs on the veins and lamina surface in the lobes; *upper surface* of costae with many acicular hairs, similar hairs occurring more sparsely on the veins and a mixture of short hairs and *minute, colourless, subsessile, gland-like capitate hairs on the lamina surface.* Sori medial or supramedial, rarely more than five pairs of veins in a lobe fertile and sori often present only on the basal veins; indusia normally sparsely pilose with long hairs but sometimes almost or quite glabrous. n = 36, diploid.

Collections: Thwaites C.P. 974 in part (CGE; PDA). *Thwaites* C.P. 714 (K; PDA, in part). Heights above Kandy, *Walker* in Herb. Hook. (K). Lady Horton's Walk, Kandy, 600 m, 11 Dec. 1950, *Sledge* 578 (BM). Same locality, 6 Feb. 1954, *Sledge* 1100, 24 March 1954, *Sledge* 1356 (BM). Roseneath Valley, Kandy, 630 m, 3 Feb. 1954, *T. G. Walker, Sledge* 1092 (BM). Kandy, Catchment on bank in secondary jungle, 750 m, 4 Feb. 1954, *Sledge* 1098 (BM). Laxapana, 900 m, 28 Jan. 1954, *Sledge* 1060 (BM). Allagalla, 600 m, 19 Feb. 1954, *Sledge* 1151 (BM). Hillside above Potupitya, Ratnapura District, forest patch, much degraded, 1500 m, 4 Dec. 1976, *Faden* 76/480 (K). Between Kirapatdeniya & Weligepola, Ratnapura District, swampy places in forest patch above road, 1900–2000 m, 30 Dec. 1976, *Faden* 76/653 (K). Unlocalised: 1899, *Bradford* (K). 1861, *Hance* 132 ex Thwaites (P). *Ferguson* [as *Nephrodium molle*] (US 816419).

Distribution imperfectly known but probably widespread; less frequent than *Christella dentata* and *C. parasitica.*

Tropics of Asia, Africa and America.

Holttum's description of *Christella hispidula* states 'Rhizome erect or short-creeping.' I believe the rhizome is *always* erect and that the apparently creeping habit displayed by some herbarium specimens is illusory. Two of my gatherings (*Sledge* 1092, 1098) would certainly be construed by most botanists as having creeping rhizomes; yet these were taken from a very steep clay bank by a road through forest. In such a position soil movement tends to cover and depress the rhizome into a horizontal position, the apex on emergence turning upwards before unfurling the tufted fronds, the excavated rhizomes thus having every appearance of being horizontally creeping. *C. hispidula* commonly grows in clearings or where circumstances allow increased light penetration, as where roads run through jungle and forest; thus there must be other gatherings which, like my own, display a similar stem apex and fronds.

Christella hispidula is easily recognised by its habit of growth and straw-coloured, hairy stipes and decrescent fronds. Living fronds are normally pale green or yellow-green, but there is little evidence in dried fronds of this colour difference. The fronds vary in size, often the stipes being short with crowded lower pinnae, but they may be over 20 cm long with the lower pinnae well spaced. They are also pinnate to the apex, rarely terminating in a pinnatifid pinna-like part as in most other Ceylon species of *Christella.* The didymosoral condition produced by only the basal pair of veins being fertile and hence giving rise to a single row of paired and closely contiguous sori on each side of the costa, commonly occurs in both *C. hispidula* and *C. parasitica,* but I have not observed it in other Ceylon species of *Christella.*

Beddome failed to distinguish *C. hispidula, C. parasitica* and *C. dentata* (see p. 31) and therefore attributed to *Nephrodium molle* a rhizome which may be either erect or creeping and fronds which may or may not be decrescent.

4. **Christella subpubescens** (Blume) Holttum (Fig. 5E)

in *Webbia* **30** : 193 (1976).—*Aspidium subpubescens* Blume, *Enum. Pl. Jav.* : 149 (1828). Type: Java, *Blume* (L : 910, 327–113, large sheet collection).—*Dryopteris subpubescens* (Blume) Christensen in *Gard. Bull. Str. Settl.* **4** : 390 (1929); *Index Fil. Suppl.* **3** : 99 (1934). Backer & Posth., *Varenfl. Java:* 65 (1939) p.p.— *Cyclosorus subpubescens* (Blume) Ching in *Bull. Fan meml Inst. Biol.* (Bot.) **8** : 211 (1938) p.p.—*Thelypteris subpubescens* (Blume) K. Iwats. in *Mem. Coll. Sci. Kyoto Univ.* B, **31** : 173 (1965), excl. syn. *Aspidium jaculosum* Christ.

Aspidium amboinense sensu Blume, *Enum. Pl. Jav.*: 148 (1828), non Willd. Kunze in *Bot. Ztg.* **6** : 261 (1848). Mettenius, *Farngatt.* pt IV : 105 (1858).—*Nephrodium amboinense* sensu Hook., *Spec. Fil.* **4** : 75 (1862); *Syn Fil.* : 292 (1867) p.p.; Bedd., *Suppl. Ferns S. Ind. & Brit. Ind.* : 19 (1876); *Handb.*; *Suppl.* : 75 (1892) p.p.—*Nephrodium molle* var. *amboinense* sensu Bedd., *Handb. Ferns Brit. Ind.* : 278 (1883), excl. syn. *Nephrodium extensum* var. *minor* Bedd.

Aspidium molle var. *latipinna* Benth., *Fl. Hongkong.* : 455 (1861). Lectotype: Hong Kong, *Hance* 135 (K).—*Nephrodium latipinna* (Benth.) Hook., in Hook. & Baker, *Syn. Fil.* : 292 (1867).—*Aspidium latipinna* (Benth.) Hance in *J. Linn. Soc.* (Bot.) **13** : 141 (1873).—*Dryopteris latipinna* (Benth.) Kuntze, *Rev. Gen. Pl.* **2** : 813 (1891). van Rosenb., *Handb. Malay. Ferns* : 217 (1908).—*Christella latipinna* (Benth.) H. Lév., *Fl. Kouy-tchéou* : 475 (1915).—*Cyclosorus latipinna* (Benth.) Tardieu in *Phanérogamie* **7** : 73 (1938). Tardieu & Christensen in Lecomte, *Fl. Gén. Indoch.* **7** (2) : 397 (1941). Holttum, *Rev. Fl. Mal.* **2** : 276, fig. 159 (1955).—*Thelypteris latipinna* (Bentham) K. Iwats. in *Acta phytotax. geobot. Kyoto* **21** : 166 (1965). Morton in *Contr. U.S. natn. Herb.* **38** : 361 (1974).

Dryopteris sumatrana van Rosenb., *Malay. Ferns* : 227 (1908) p. maj. p. Type: Sumatra, 1778, *C. Miller* (BM).—*Cyclosorus sumatranus* (van Rosenb.) Ching in *Bull. Fan meml Inst. Biol.* (Bot.) **10** : 249 (1941). Holttum, *Rev. Fl. Mal.* **2** : 275, fig. 158 (1955).—*Thelypteris sumatrana* (van Rosenb.) Tagawa & K. Iwats. in *Acta Phytotax. Geobot. Kyoto* **22** : 101 (1967).

Nephrodium molle var. *major* Bedd., *Handb. Suppl.* : 76 (1892) quoad pl. Sumatr. tantum.—*Dryopteris subpubescens* var. *major* (Bedd.) Christensen in *Gard. Bull. Str. Settl.* **4** : 390 (1929).

Dryopteris pseudoamboinensis Rosenst., *Meded. Rijks.* **31** : 7 (1917). Lectotype (selected by Panigrahi): Sumatra, *Korthals* 270 (L.).—*Thelypteris pseudoamboinensis* (Rosenst.) Panigrahi in *Phytologia* **30** : 410, pl. 111 (1975).

Thelypteris blumei Panigrahi in *Phytologia* **30** : 409 (1975); *op. cit.* **31** : 369 (1975).

Rhizome short-creeping; stipes up to 30 cm long, scaly below, thinly pubescent above; rhachis hairy on the upper surface, subglabrous beneath. Lamina up to 80 cm long, pinnate with up to 20 pairs of free pinnae below the pinnatifid apex, lower 2–4 pairs gradually reduced and widely spaced, the basal acroscopic lobes of the lower pinnae enlarged with forked and often anastomosing veins. Pinnae up to $12 \times 1\frac{1}{2}$ cm, base truncate, apex acuminate, *lobed from $\frac{1}{4}$ to less than half way to costa,* veins 4–8 pairs in the lobes, *excurrent vein* from the union of the lowermost veins of adjacent lobes *joined below or at the base of the sinus* by *the second pair of veins,* the next acroscopic vein often reaching the base of the sinus in large pinnae; *lower surface of pinnae with scattered short hairs mainly on the costae and veins*; upper surface of costae and veins with short acicular hairs, elsewhere surfaces glabrous. Sori medial; indusia normally glabrous but often short-hairy. $n = 72$ tetraploid.

Collection: Kadugannawa, amongst undergrowth below *Hevea* trees near roadside, 300 m, 12 Dec. 1950, *Sledge* 585 (BM).

Apparently very rare but perhaps overlooked through confusion with other species.

Also in north-east India to south China, Burma, Thailand, Vietnam, Malaysia to New Guinea, Philippines and Fiji.

Christella subpubescens differs from *C. dentata* and allied species in its less deeply divided and less hairy pinnae. I have not been able to detect the very short capitate hairs which Holttum says are usually present on the lower surfaces of the pinnae and the very minute hairs—best seen with a binocular—which seem normally to be present on the lamina surface in this species are not evident in my specimen. The indusia of my gathering are also glabrous, but they are hairy in an example sent from Singapore by Holttum. The pinnae are more deeply lobed than in most examples of *C. subpubescens,* but in their venation and other respects they are typical. Holttum has seen the gathering and confirmed the identification.

Beddome cited no Ceylon stations for *Nephrodium amboinense,* which is not figured in his two volumes of illustrations, but it should be noted that in the *Supplement to the Ferns of Southern India and British India.* : 19 (1876) he distinguished between *C. subpubescens* and *C. zeylanica*—as *Nephrodium amboinense* and *N. amboinense* var. *minor* respectively—giving the distribution of the former as north India and Ceylon and of the latter as Ceylon only. Later, in his *Handbook* and its *Supplement,* the two were no longer treated as distinct from one another.

In his *Ferns of Malaya* (*Rev. Fl. Mal.* **2** : 276 (1955)) Holttum states that *Cyclosorus latipinna* 'certainly occurs in Assam and Ceylon' though in his paper on *Christella* (*Kew Bull.* **31** : 293–339 (1976)), where *C. latipinna* is treated as synonymous with *C. subpubescens,* Ceylon is not included in the distribution. It is probable that the species occurs elsewhere than at Kadugannawa although it must be rare since I have seen no other gathering amongst the extensive herbarium material examined. It has not been recorded from southern India and the distribution attributed to it by Holttum suggests that in Ceylon it is at the westernmost extremity of its range.

5. **Christella meeboldii** (Rosenst.) Holttum (Fig. 5F)

in Nayar & Kaur, *Companion Beddome* : 208 (1974); *Fl. Hassan Dist.* : 860 (1976).—*Dryopteris meeboldii* Rosenst. in *Reprium Spec. nov. Regni veg.* **12** : 247 (1913). Christensen, *Index Fil. Suppl.* **2** : 15 (1917). Type: Southern India, Tellicherry, *Meebold* 2133 (WRSL).—*Cyclosorus meeboldii* (Rosenst.) Ching in *Bull. Fan meml Inst. Biol.* (Bot.) **8** : 210 (1938), excl. *Stocks & Law* spec. ex 'Malabar'.—*Thelypteris meeboldii* (Rosent.) C. F. Reed in *Phytologia* **17** : 291 (1968).
Christella malabariensis (Fée) Holttum in *Kew Bull.* **31** : 317 (1976) p.p.

Rhizome short-creeping, clothed about the apex and on the lower parts of the stipes with lanceolate, long-attenuate, brown scales; fronds 30–60 cm long, up to 15 cm broad, pinnate with about 15 pairs of free sessile pinnae below the narrowly deltoid, deeply lobed apex, lower 2–4 pairs reduced in size and deflexed, basal acroscopic lobes of lower pinnae slightly enlarged; largest pinnae 5–8·5 × 1–1·5 cm, *lobed from* $\frac{1}{3}$ *to nearly half way to the costa,* the lobes broadly rounded to truncate with forward-pointing tips, veins 5–8 pairs in the lobes $1\frac{1}{2}$–2 pairs anastomosing, apex of pinnae entire, acute or acuminate, base truncate or obliquely truncate; upper part of stipe and rhachis with spreading hairs, *lower surface of pinnae with short, spreading hairs on the costa, costules, veins and margins of segments* and a few longer, acicular hairs on the costa, upper surface hairy on the costa and veins, minutely hairy on the surfaces and, at least when young, with scattered, short, capitate hairs especially in the basal regions of the pinnae; sori medial to supramedial, the lowest on veins from adjacent costules often touching or merging; indusia glabrous or with a few hairs; *spores verrucose.*

Collections: Near Badulla road [from Hakgala], open ground, 29 Dec. 1950, *Ballard* 1315 (K). Near Parawella Falls, Kandapola, Nuwara Eliya, 1450 m, 19 March 1954, *Sledge* 1327 (BM).

Distribution in Ceylon not known; probably of rare occurrence.
Also in southern India.

In his account of the genus *Christella,* Holttum reduced *C. meeboldii* to a synonym of *C. malabariensis.* I have shown elsewhere (*Kew Bull.* **34** : 77–81 (1979)) that Fée's *Nephrodium malabariense* is the same as *Christella dentata,* though Holttum included *dentata-parasitica* hybrids in his concept of *C. malabariensis.* However, Meebold's gathering from southern India, on which Rosenstock based his species, had not been seen by Holttum for his paper. An isotype was subsequently traced to and obtained from Wroclaw, and a photograph and description of this were sent to me. Ching had also treated Meebold's gathering, and the Stocks and Law specimens on one of which Fée based his *Nephrodium malabariense,* as belonging to the same taxon, for which however he used the name *Cyclosorus meeboldii.* I followed Holttum and Ching in my paper on the identity of Fée's species in not treating *Christella meeboldii* as distinct from the Stocks and Law plants.

My Kandapola gathering, which differs from all other Ceylon species save *Christella papilio* in having verrucose spores, had been set aside as a presumed new species. The shallow lobing of the pinnae, however, often with two pairs of veins anastomosing well below the sinus membrane, matched that of Meebold's south Indian plant. Since no information was available about the spores of *C. meeboldii,* the Wroclaw specimen was again sent for and this also proved to have verrucose spores. This both fixed the identity of my own plant, whilst providing a sure way of distinguishing *C. meeboldii* from all other species of *Christella* in Ceylon, for although it has the same type of spore ornamentation as in *C. papilio,* there is no similarity between the fronds of these species.

Forms of *Christella dentata* occur in which the pinnae are cut less than half way down and such forms approach *C. meeboldii* in appearance, though they rarely if ever have two pairs of veins fully confluent below the sinus membrane. In *C. meeboldii* the uppermost sori in the pinna segments are medial in position, and successive pairs tend to diverge downwards so that the sori on the lowermost acroscopic and basiscopic veins of adjacent segments are closely contiguous, and hence the rows of sori in fully fertile fronds form an inverted V-shape. Rarely there may be a single sorus at the point of anastomosis or it may even be inserted on the excurrent vein. The indusia are sparsely hairy or glabrous. Though some of these characters may be found in the variable *C. dentata,* they are never combined in any form of that species.

From *Christella subpubescens,* which it most closely resembles in its shallow lobing and venation *C. meeboldii* differs in its hairy fronds. Fortunately the distinctive spores of *C. meeboldii* afford a means of identification if macroscopic characters remain doubtful.

6. **Christella papilio** (Hope) Holttum

in Nayar & Kaur, *Companion Beddome* : 208 (1974).—*Nephrodium papilio* Hope in *J. Bombay nat. Hist. Soc.* **12** : 625, t.12 (1899). Lectotype: India, Darjeeling, 1880, *Levinge* (K).—*Dryopteris papilio* (Hope) Christensen, *Index Fil.* : 282 (1905).—*Cyclosorus papilio* (Hope) Ching in *Bull. Fan meml Inst. Biol.* (Bot.) **8** : 214 (1938).—*Thelypteris papilio* (Hope) K. Iwats. in *Mem. Coll. Sci. Kyoto Univ.* B, **31** : 175 (1965).

Aspidium extensum sensu Thwaites, *Enum. Pl. Zeyl.* : 391 (1864) quoad C.P. 3498, non Blume.
Nephrodium molle var. *major* Bedd., *Handb. Suppl.* : 76 (1892)excl. pl. ex Sumatra.

Rhizome erect or (var. *repens*) short-creeping; stipes up to 20 cm, stramineous, scaly at the base, glabrous above. Fronds (including stipes) up to 120 cm, decrescent, pinnate with about 20 pairs of free pinnae beneath the pinnatifid terminal pinna, largest pinnae commonly 10 × 1·5 cm but up to twice as long and proportionately wider, caudate-acuminate, *lobed from one third to half way to the costa, lower 5–12 pairs of pinnae much shortened,* well spaced, *mostly broadly triangular in outline* with basal acroscopic lobes enlarged and sometimes free almost to the base; veins 6–9 pairs in the lobes 1½–2 *pairs anastomising,* texture herbaceous; *surfaces apparently glabrous* save on the costa above *but minute hairs present on the lamina surface above and below,* a few scattered short hairs on the veins and, very rarely, sessile yellow glands beneath. Sori medial; indusia usually short-hairy, sometimes glabrous; *spores verrucose.*
var. **papilio** Rhizome erect. Diploid.

Collection: Thwaites C.P. 3498 (PDA). *Sub Nephrodium amboinense,* on same sheet as *C. zeylanica* (PDA).

var. **repens** Sledge, **var. nov.**

Thelypteris taprobanica Panigrahi, *Kew Bull.* **31** : 187 (1976) p.p. Type: Ceylon, *Wall* (K, isotype).

Rhizoma repens : chromosomatum numerus tetraploideus.

Collections: Hakgala, by jungle stream, 1650 m, 27 Dec. 1950, *Sledge* 744 (BM). Below Hakgala Gardens, jungle, 1650 m, 26 Feb. 1954, *Sledge* 1212 (BM, holotype). Tangamalai Sanctuary, Haputale, 1500 m, 25 Feb. 1954, *Sledge* 1205 (BM) *Unlocalised: Wall* (K).
Specimens lacking rhizomes: *Thwaites* C.P. 3498 (BM; CGE; K; P; PDA). 1819, *Moon* (BM). Ambawella, *Wall* (K), *Ferguson* (US 826085).

By streams in forest in the higher parts of Central and Uva Provinces. Also in southern India and north-west Himalayas eastwards to Sikkim, Thailand, northern Malaysia and Taiwan.

Hope's species, as described from north-west India, is readily recognised by its erect, and often emergent, rhizomes and its almost glabrous, strongly decrescent fronds in which the lower pinnae are reduced progressively to short, deltoid, auricled appendages arranged in opposite, and hence butterfly-like, pairs. Hope included Ceylon in the distribution of *Christella papilio,* accepting specimens of *Thwaites* C.P. 3498 and of G. Wall as identical with his new species, though these gatherings are lacking rhizomes. Beddome (in *Handb. Suppl.* : 76 (1892) had stated that 'Mr Wall's Ceylon specimens however have a decidedly creeping root' and when Hope saw the Ceylon specimens to which Beddome referred, he expressed the view that despite the similarity of their fronds 'the creeping rhizome I consider quite enough to separate them . . . from *N. papilio.*'

Very few herbarium specimens from Ceylon include rhizomes and where these are present they are short-creeping, as in my own three gatherings. There are, however, in the Peradeniya collection, two specimens which plainly show vertically erect rhizomes, and plants with erect rhizomes also occur in southern India (*Gamble* 11698 and 11769, Nilgiris District, 1883 (K)). The Peradeniya specimens are the only ones from Ceylon with erect rhizomes seen by me in the numerous sheets examined from many herbaria.

Manton (in Manton & Sledge, *Phil. Trans. R. Soc.* **238** : 138 (1954)) found that a Ceylon plant (with creeping rhizome) was tetraploid (n = 72), whereas Loyal (in *Proc. 48th Indian Sci. Congr.* Pt. 3 : 266–267 (1961)) has shown that plants from east and west Himalayas (presumably with erect rhizomes) are diploid (n = 36). I can find no frond or spore characters consistently linked with an erect or with a creeping rhizome which would serve as a means of distinguishing between diploid and tetraploid in the absence of basal parts. The inclusion of Ceylon moreover within the distributional range of *Christella papilio* by Ching (in *Bull. Fan meml Inst. Biol.* (Bot.) **8** : 24 (1938)) and Holttum (*Kew Bull.* **3** : 322 (1976)) (underlines the fact, first recognised by Hope, that it is not possible to distinguish isolated fronds derived from plants with the different growth habits.

In the same issue of the *Journal of the Bombay Natural History Society* as that in which Hope described *Nephrodium papilio,* another new species *Polypodium late-repens* is described, differing from the erect-growing *P. distans* D. Don (= *Pseudophegopteris pyrrhorhachis* (Kunze) Ching) in its widely creeping and branched rhizome. But Holttum (*Blumea* **17** : 24 (1969)) treats the former as a synonym of the latter on the grounds that 'I can see no distinction between specimens lacking rhizomes.' The situation is closely parallel in the case of *Christella papilio* from northern India and Ceylon, save for the known cytological difference, and this in conjunction with the difference in growth habit justifies nomenclatural recognition at varietal level, although as most herbarium specimens lack basal parts, only the aggregate name can be given.

The position has recently been confused rather than clarified by Panigrahi's (*Kew Bull.* **31** : 187–188 (1976)) description of *Thelypteris taprobanica.* Knowing that Ceylon plants differ from Hope's *Christella papilio* in their creeping habit and in their cytology, he evidently extracted from the Ceylon *C. papilio* cover at Kew the three specimens which showed a creeping rhizome and based his new species on these specimens. However, two of these, including his holotype, should not have been included under *C. papilio* for they are, in fact, specimens of *C. dentata.* They both lack the numerous and characteristic triangular-deltoid, reduced, auriculate and butterfly-like lower pinnae and both have the ridged spore ornamentation of *C. dentata.* The third specimen (Panigrahi's 'isotype') is manifestly different, having the short, broad lower pinnae of *C. papilio* and verrucose spores as illustrated by Wood in *Bot. J. Linn. Soc.* **67** (Suppl. 1): 194, pl. 1E (1973). Panigrahi's description moreover 'whole frond glabrous' and 'indusium glabrous' is applicable to only one of the three specimens; two have hirsute indusia and one is hairy on the lower surface. Holttum overlooked Panigrahi's error and has recognised his species as *Christella taprobanica* in his account of the genus.

Holttum (*loc. cit.*) states that specimens of *Christella papilio* from Thailand and Malaya may be glandular on the lower surface of the fronds, but no such glandular specimens had been seen by him from India. Ferguson's specimen in US., named *Nephrodium amboinense* and misidentified by Ching and Iwatsuki as *Cyclosorus subpubescens,* is studded below with abundant, sessile, yellow glands. I have seen no other glandular specimen of *C. papilio* from Ceylon.

7. **Christella zeylanica** (Fée) Holttum

in Nayar and Kaur, *Companion Beddome* : 208 (1974).—*Nephrodium zeylanicum* Fée, *Mem. Fam. Foug.***10** : 42 (1865). Type: Ceylon, *Thwaites* C.P. 3391 (holotype not seen; BM, CGE, K (errore 3390), PDA, isotypes).

Aspidium extensum sensu Thwaites, *Enum. Pl. Zeyl.* : 391 (1864) quoad C.P. 3391 non Blume.

Nephrodium extensum var. *minor* Bedd., *Ferns Brit. Ind.* : t.201 (poor) (1866). Type: Ceylon, *Thwaites* (K).—*Nephrodium amboinense* var. *minor* (Bedd.) Bedd., *Suppl. Ferns S. Ind. & Brit. Ind.* : 19 (1876).

Nephrodium molle var. *amboinense* sensu Bedd., *Handb. Ferns Brit. Ind.* : 278 (1883) p.p.—*Nephrodium amboinense* sensu Bedd., *Handb. Suppl.* : 75(1892) p.p.

Thelypteris srilankensis Panigrahi in *Notes R. bot. Gdn. Edinb.* **33** : 499 (1975). Type: as for *C. zeylanica.*

Rhizome short-creeping; fronds up to 60 cm long including stipe but commonly less; stipe to 9 cm, scaly at the base, elsewhere *glabrous as is the rhachis* save for scattered hairs in the dorsal groove especially distally on the rhachis. Lamina with up to 20 pairs of free *subentire pinnae* beneath the well-marked terminal pinnatifid pinna which may be up to 13 cm long; *lower 3–6 pairs of pinnae gradually reduced,* the lowermost 1–2 cm long; pinnae up to 9 × 1·2 cm, acuminate, *edges crenate,* veins 3–5 pairs, 1½–2 pairs anastomosing, *lower surface glabrous* save for minute, gland-like, capitate hairs when young, glabrescent later, *upper surface with scattered hairs on the costae,* elsewhere glabrous. Sori medial, 1–2 pairs of veins fertile; indusia glabrous.

Collections: Thwaites C.P. 3391 (BM; CGE; K (errore 3390); P; PDA). 1887, *Wall* (P.)
Kitulgala, 150 m, Sabaragamuwa Province.

Ceylon and (*teste* Holttum) Nicobar Islands.

Christella zeylanica is a very distinct species, differentiated from all other Ceylonese species of the genus by its subentire to crenate, nearly glabrous pinnae. In appearance it resembles a small form of *Sphaerostephanos arbuscula* more than the other species of *Christella.* It is related to *C. subpubescens,* with which it was included by Beddome in his *Handbook* (as *Nephrodium molle* var. *amboinense* or *N. amboinense*).

Before Fée or Beddome had described this species, Thwaites (*Enum. Pl. Zeyl.* : 391 (1864)) had cited C.P. 3391 and C.P. 3498 as *Aspidium extensum* Blume (= *Amphineuron opulentum* (Kaulf.) Holttum), gatherings of the *Amphineuron* being cited under *Aspidium ochthodes* Kunze (*loc. cit.* : 392). There are two good sheets of C.P. 3391 in the Peradeniya Collection, named *Nephrodium amboinense* Presl, which doubtless represent the original gatherings. These are labelled 'Kittool Galle, Ap. 1855'. Wall, who knew it in this locality, followed Thwaites in including the distinct but as yet undescribed *Christella papilio* with it (*Cat. Ceylon Ferns* : 6 (1873)), using the name *Nephrodium amboinense* to cover both. A year after Fée described *N. zeylanicum,* Beddome described the same species as *N. extensum* var. *minor,* subsequently (*loc. cit.* 1876) transferring the variety to *N. amboinense.* Later still he dropped the variety, combining *Christella zeylanica* and *C. subpubescens* in his *Handbook* under the epithet *amboinense,* at first as a variety of *Nephrodium molle* and then, in the *Supplement,* as an independent species. Ceylon botanists, however, to whom *Christella subpubescens* was unknown, construed *Nephrodium amboinense* differently, to cover *Christella zeylanica* and *C. papilio.* The Peradeniya sheets of these species bearing Thwaites's original nomenclature of the *Enumeratio* are renamed *Nephrodium amboinense,* and despite the wide disparity between them both are, in one instance, mounted on the same sheet. *Christella papilio* remained undescribed until 1899, C.P. 3498 being included by Beddome in his *Handbook* under *Nephrodium procurrens* and in the *Supplement* to his *Handbook* under *N. molle* var. *major.*

Though Thwaites cited Uva Province as the locality for C.P. 3391 and C.P. 3498, it was in fact the source only of the latter; there is no evidence that *Christella zeylanica* has ever been collected anywhere but about Kitulgala, nor has it been refound there in the present century.

Hybrids

Cytological evidence proving the occurrence of hybrids in wild populations of *Christella* was first demonstrated by Manton (in Manton & Sledge, *Phil. Trans. R. Soc. Lond.* B, **238** : 127–185 (1954)). That hybridisation is probably of frequent occurrence was suggested by the fact that of 18 plants investigated, five of them, from four different stations, gave triploid counts or revealed meiotic irregularities. Hybrids within the *C. parasitica* group have also been synthesised experimentally by Panigrahi & Manton (*J. Linn. Soc.* (Bot.) **55** : 729–743 (1958)). They have shown that since some important distinguishing characters behave as simple dominants in F1 hybrids, such hybrids may bear so close a resemblance to one only of the two parent species as to make recognition difficult in the absence of cytological evidence. They found dominant characters to be a creeping, as opposed to an erect rhizome, non-decrescent versus decrescent frond and presence of subfoliar glands as opposed to their absence. Depth of cutting of pinnae, number of anastomosing veins, and hair length did not behave as simple dominants or recessives, and hence F1 hybrids were intermediate between the parents in these characters.

Plants with mixed characters are not uncommon in herbaria, and such specimens are best regarded as hybrids. In Panigrahi & Manton's experiments it was found that all the F1 hybrids they produced showed a high proportion of abortive spores, and they considered that spore sterility would be an effective means of detecting hybridity in a herbarium specimen. The converse, however, that good spores disprove hybrid origin, cannot be true since three of the hybrid plants listed by Manton (in Manton & Sledge, *op. cit.* 138) were retained in cultivation at Kew, and fronds taken a year or two later by Alston from two of these showed sound spores. I believe also that more evidence is required to confirm the dominance of non-decrescence, for as Holttum has commented (in *Kew Bull.* **31** : 295 (1976)), this is a surprising and unexpected finding in a group where non-decrescence is a very much less frequent condition than decrescence.

1. Christella dentata × parasitica

C. malabariensis sensu Holttum in *Kew Bull.* **31** : 317 (1976) p.p., non *Nephrodium malabariense* Fée.

Frond outline of *Christella dentata,* but one pair only of reduced and deflexed pinnae; pinnae with abundant *parasiticus* glands below, one pair of veins anastomosing, short-hairy beneath, without acicular hairs, some capitate hairs above; indusium hairy.

Collection: Near Ginigathena, Central Province, 600 m, Dec. 1950, *Manton* Z 30; *Alston* 11745 ex Trop. Fern House, Kew (BM).

Since *Christella dentata* and *C. parasitica* are the commonest species of *Christella* in Ceylon and India where they often grow together, this is almost certainly the most frequently occurring hybrid. The above description is taken from the cultivated plant which shows good evidence of each species; it also agrees with Panigrahi & Manton's statement as to non-decrescence of the frond being a dominant character, but disagrees with them in having good spores. I accept as the same hybrid specimens in which the pinnae are glandular beneath, but more than one pair of lower pinnae is shortened. Such plants were included amongst the specimens distributed by Kew as *Nephrodium molle* coll. Stocks & Law and these were in my opinion wrongly included by Holttum in Fée's *N. malabariense.* A full discussion of this matter is given in my paper in *Kew Bull.* **34** : 77–81 (1979).

It is probable that several forms of this hybrid exist. From Lady Horton's Walk, Kandy, I have two gatherings (509 and 1357) which may be hybrids of the same parentage, though they are very different from the Ginigathena plant. In both gatherings the fronds are set 2–3 cm apart on a wide-creeping rhizome, and both have abortive sporangia and spores. These are *Nephrodium procurrens* sensu Baker (*Syn. Fil.* : 290 (1867)) and of Beddome's *Handbook* (278 (1883)), which later authors have referred either to *Christella dentata* (e.g. Ching in *Bull. Fan meml Inst. Biol.* (Bot.) **8** : 207 (1938)) or to *C. parasitica* (e.g. Holttum in *Kew Bull.* **31** : 309 (1976)). If the long-creeping rhizome and sterility denote a hybrid origin, then *C. dentata* × *parasitica* would seem to be the only possible parentage, though the absence of glands, long acicular hairs or capitate hairs or any other character indicative of *parasitica* makes such an identification doubtful.

2. Christella hispidula × parasitica

Frond outline of *Christella parasitica* with lowest pair only of pinnae somewhat shortened; one pair of veins anastomosing, the second pair reaching margins well above base of sinus; pinnae eglandular beneath rather thinly hairy on costae and veins and on indusia, without long acicular hairs. Sporangia mostly abortive; no good spores.

Collection: Lady Horton's Walk, Kandy, 600 m, Dec. 1950, *Manton* P43; *Alston* 11742 ex Trop. Fern House, Kew (BM).

This plant was a triploid with N pairs and N singles. The frond taken by Alston from the cultivated stock agrees well with Panigrahi & Manton's silhouette (*loc. cit.* fig. 4) of a synthesised hybrid of the same parentage, save that the lowermost pair of pinnae is somewhat shorter than the next pair. The absence of subfoliar glands in the wild hybrid is presumably due to the *Christella parasitica* parent, in this instance being an eglandular form of the species. Both parents and *C. dentata* are frequent on the wooded hillside of Lady Horton's Walk but the venation and triploid cytology would appear to rule out *C. dentata* as the second parent.

3. Christella meeboldii × parasitica

Rhizome 'sub-erect to short-creeping'; fronds decrescent with three to six pairs of progressively reduced pinnae; pinnae cut less than half way to costa, short-hairy on costa and veins above and below, without acicular hairs but with abundant *parasiticus* glands beneath, two pairs of veins anastomosing; indusia glabrous or nearly so; spores ± verrucose or shortly ridged.

Collection: Hangiliella beyond Welimada on Badulla road from Nuwara Eliya, *c.* 900 m, 29 Dec. 1950, *Manton* P. 307; *Alston* 11737 ex Trop. Fern House, Kew (BM).

The mixed characters of this plant seem only explicable on the assumption of the above parentage, and that non-decrescence of the frond is not a dominant character in this hybrid combination. Typical *C. meeboldii* and *C. parasitica* were both collected here by Ballard.

XIII. PNEUMATOPTERIS Nakai

in *Bot. Mag. Tokyo* **47** : 179 (1933), emend. Holttum in *Blumea* **19** : 42 (excl. *Pseudocyclosorus*) (1971); *op. cit.* **21** : 293 (1973).

Caudex usually erect, rarely creeping; rhizome scales broad, thin, with marginal hairs; fronds pinnate, usually large, decrescent, with shallowly to deeply lobed pinnae, the lobes with cartilaginous margins; usually several pairs of basal pinnae reduced either abruptly or gradually; aerophores on reduced and lower pinnae distinct, ± swollen; stipe and lamina never conspicuously hairy; veins in most species anastomosing, free in a few species; lamina between veins ± pustular when dry, sessile spherical glands never present; sori usually indusiate, sporangia often bearing short, club-shaped, glandular hairs, stalks with a 2–4 celled hair with enlarged terminal cell; spores pale with many small ± quadrate wings of irregular shape, hence spinulose in aspect. n = 36.

About 75 species; mainly in Malesia with a few species in Africa and the Mascarene Islands; mainland Asia from southern China southwards throughout Malesia to Australia (northern Queensland) and New Zealand, and in the Pacific Islands from Fiji and Samoa to Hawaii.

1. **Pneumatopteris truncata** (Poiret) Holttum

in *Blumea* **21** : 314 (1973).—*Polypodium truncatum* Poiret, *Encycl. Meth.* **5** : 534 (1804). Type: Brazil [no collector's name] (P).—*Cyclosorus truncatus* (Poiret) Farwell, *Am. Midl. Nat.* **12** : 250 (1931). Ching in *Bull. Fan meml Inst. Biol.* (Bot.) **8** : 216 (1938).

Nephrodium truncatum sensu Bedd., *Handb. Ferns Brit. India* : 280 (1883), non (Gaudich.) C. Presl.

Aspidium abortivum Blume, *Enum. Pl. Jav.* : 154 (1828). Type: Java, *Blume* (L).

Aspidium abruptum Blume, *Enum. Pl. Jav.* : 154 (1828). Type: Java, *Kuhl & van Hasselt* (L).—*Nephrodium abruptum* (Blume) J.Sm. in *Hooker's J. Bot.* **3** : 411 (1841). Hook., *Spec. Fil.* **4** : 77 (1862) p.p. et excl. t.241 B.

Aspidium eusorum Thwaites, *Enum. Pl. Zeyl.* : 391 (1864). Type: Ceylon, *Thwaites* C.P. 3064 (K).—*Nephrodium eusorum* (Thwaites) Bedd., *Ferns Brit. India* : t.130 (1866) [Illustration of *Beddome* (K)].

Rhizome erect, fronds tufted, from 90–240 cm long; stipe and rhachis pale, puberulous at first, becoming glabrous; lamina 60–120 × 30–60 cm, bipinnatifid with 20–30 pairs of pinnae and *up to 8 pairs of abruptly reduced lower ones forming widely spaced auricles along the stipe*; pinnae up to 30 × 3 cm in large fronds, 15 × 1·5–2 cm in small ones, apex acuminate, base truncate in the upper pinnae becoming contracted below and shallowly lobed in the lower pinnae, margins lobed up to $\frac{1}{2}$ way to the costa, the *lobes oblong and slightly crenated about the subtruncate apices*; veins up to 10 pairs, *strongly raised beneath*, $1\frac{1}{2}$–$2\frac{1}{2}$ pairs anastomosing; upper surface of costae sparsely hairy otherwise *surfaces glabrous above and below* but *with pustular swellings beneath* when dry; sori medial, forming two parallel rows, the lower ones not divergent; indusia glabrous, small, evanescent.

Collections: Thwaites C.P. 3064 (CGE; K; P; PDA). Hantane Range, in forests, July 1844, *Gardner* 1104 (BM; CGE; K). Kadugannawa, shady forest, Oct. 1846, *Gardner* 1252 (CGE, K). Oodawella, 1870, leg. *Randall* in herb. Rawson 3244 (BM). Gallebodde, Central Province, by stream in jungle, 600 m, 26 Jan. 1954, *Sledge* 1046 (BM). Between Gilimale and Carney, Ratnapura District, jungle, 150 m, 9 March 1954, *Sledge* 1250 (BM). Sinha Raja Forest above Beverley Estate, Deniyaya, 900 m, 12 March 1954, *Sledge* 1277 (BM). Lady Horton's Walk, Kandy, 600 m, 24 March 1954, *Sledge* 1355 (BM). Unlocalised: *Beddome* (K). 1887, *Wall* (P). *Mrs Chevalier* (BM). *Macrae* (CGE). *Bradford* (CGE). *Walker* (K).

In forests of the interior to 1500 m.

Also in southern and north-east India, southern China, western Malesia and the Philippine Islands.

A large fern, in facies most resembling *Pronephrium articulatum* and confused with that species by some early botanists. It is readily distinguished by its decrescent fronds with 1–2 pairs of anastomosing veins in the glabrous pinnae, as opposed to the non-decrescent, glandular fronds of *P. articulatum,* with at least 3 and commonly 4–6 pairs of anastomosing veins.

XIV. SPHAEROSTEPHANOS J.Sm.

in Hook., *Gen. Fil.* : t.24 (1839). Holttum in *Blumea* **19** : 39 (1971).

Caudex erect to long-creeping; fronds decrescent with varying number of much-reduced basal pinnae; pinnae pinnatifid to shallowly lobed; aerophores at base of pinnae often swollen; veins anastomosing or rarely free, surfaces always ± hairy and sessile spherical glands commonly present on lower or both surfaces; sori round or in a few species ± elongate, usually indusiate; indusia often hairy and/or glandular; sporangia usually bearing spherical glands or setae near the annulus, the stalks bearing a multicellular hair with swollen end-cell; spores light brown, spinulose or bearing many small translucent wings. $n = 36$.

About 150 species: mainly in New Guinea and the Philippine Islands with a few species in Madagascar, Mascarene Islands, southern India and Ceylon, Burma, southern China and throughout Malesia eastwards across the Pacific to Tahiti. Outlying stations in São Tomé, east Africa, New Caledonia and Australia.

1. **Sphaerostephanos arbuscula** (Willd.) Holttum

in *Jl. S. Afr. Bot.* **40** : 164 (1974).—*Aspidium arbuscula* Willd. in L., *Sp. Pl.* 4th ed., **5** : 233 (1810). Type: Mauritius. *Herb. Willd.* 19,763 (B).—*Nephrodium arbuscula* (Willd.) Desvaux in *Mém. Soc. linn. Paris* **6** : 253 (1827). Beddome. *Handb. Ferns Brit. Ind.* : 276, fig. 142 (1883).—*Dryopteris arbuscula* (Willd.) Kuntze, *Rev. Gen. Pl.* **2** : 812 (1891).—*Cyclosorus arbuscula* (Willd.) Ching in *Bull. Fan meml inst. Biol.* (Bot.) **8** : 194 (1938).—*Thelypteris arbuscula* (Willd.) K. Iwats. in *Acta phytotax. geobot. Kyoto* **21** : 170 (1965).

Rhizome *erect,* often emergent and trunk-like; stipe and rhachis grey-pubescent, the stipe short and scaly at the base; fronds tufted, commonly 30–60 cm but sometimes reaching 1 m or more, 10–20 cm wide, oblong-lanceolate in outline and narrowing towards both extremities, pinnate with numerous pairs of narrowly oblong, acuminate pinnae often auricled at the acroscopic base, *margins crenate or serrate,* up to 10 pairs and sometimes more of the lower pinnae *gradually reduced to deltoid auricles* and extending nearly or quite to the base of the stipe; veins 4–6 pairs the lowermost 1–1½ pairs anastomosing and forming an excurrent nerve, the next pair running to the long sinus membrane; texture herbaceous; upper surface of pinnae glabrous with age save on the costa, *lower surface* hairy on the costa, costules and veins and *dotted with spherical, sessile, yellow glands*; sori medial on the veins, indusium glandular with few or many hairs; sporangia with yellow glands near the annulus.

Collections: Thwaites C.P. 1359 (BM; CGE; K; P; PDA). Rambodde, shady banks, June 1845, *Gardner* 1109 (CGE; K). Kadugannawa, moist woods, Oct. 1846, *Gardner* 1251 (CGE). Adam's Peak, 14 Feb. 1908, *Matthew* (K). Kotmalee, 1847, *Fortescue* (CGE). Badulla, *Freeman* 264, 265 (BM). 1870, 1871, Oodawella, *Randall* in herb. Rawson 3220 (BM). Kandy, 1854, *Bradford* (BM; CGE; P). Hunnasgiriya, 18 Jan. 1954, *Schmid* 951 (BM). Galaha 940 m, 22 Jan. 1954, *Schmid* 1036 (BM). Deniyaya, 550 m, 5 Feb. 1954, *Schmid* 1145 (BM). Balangoda-Rassagala road, Ratnapura Dist., in lowland forest, *c.* 750 m, 16 Nov. 1976, *Faden* 76/306 (K). Above Pinnawala on Balangoda road, rocky creek in forest, 19 March 1968, *Comanor* 1090 (US). Corbet's Gap, 1200–1300 m, 9 Dec. 1950, *Sledge* 553, 557 (BM). Same locality, 1200 m, 7 Jan. 1951, *Sledge* 854 (BM). Ramboda Pass, 1560 m, 17 Dec. 1950, *Sledge* 660 (BM). Hunnasgiriya, open ground by stream, 870 m, 16 Jan. 1954, *Sledge* 969 (BM). Ambagamuwa, marsh in jungle, 570 m, 19 Jan. 1954, *Sledge* 993 (BM). Unlocalised: *Walker* (K). *Robinson* 150 (K). *Geo. Wall* (P; PDA). *Ferguson* (PDA; US 816397).

Common on banks of streams and in wet ground in forests in the interior from 550–1550 m.

Southern India, Ceylon, Mascarene Islands, Madagascar and, as subsp. *africanus* Holttum, Tanzania and Kenya.

This species and *Sphaerostephanos unitus* are two of the most frequently occurring thelypteroid ferns in the hill country of Ceylon. Several other species with anastomosing veins have coloured glands on or between the veins on the under surface of the pinnae, but the species of *Sphaerostephanos* are the only ones in which this character is combined with decrescent fronds.

2. **Sphaerostephanos subtruncatus** (Bory) Holttum

in *Kew Bull.* **26** : 80 (1971).—*Polypodium subtruncatum* Bory in Bélanger, *Voy. Ind. Or.* (Bot.) **2** : 32 (1833). Type: India, Madura, Mts de Dendigall, *Bélanger* (P).

Dryopteris mauritiana var. *gardineri* Christensen in *Trans. Linn. Soc.* (Bot.) II, **7** : 413 (1912). Type: Seychelles, *J. S. Gardiner* (K).

Rhizome erect, fronds tufted, up to 2 m tall; stipe 40–60 cm long, dark coloured, tetragonal, scaly near the base, elsewhere glabrous or nearly so, bearing *about 15 pairs of contracted pinnae,* the *lower ones reduced to mere papillate protuberances*; lamina elliptic-lanceolate, 75–120 cm with 30 or more pairs of pinnae, the *transition between normal and reduced pinnae abrupt*; pinnae up to 16 × 1·5 cm sessile, bearing a brown aerophore at junction with rhachis, apex acuminate, *margins lobed half way to costa,* lobes blunt, slightly falcate; veins 5–8 pairs in each lobe, $1\frac{1}{2}$ pairs anastomosing $\frac{1}{2}$–1 pair to base of sinus; costae and costules hairy above and below, scattered hairs on the veins and *numerous sessile, spherical, yellow glands present throughout lower surface*; texture firm herbaceous; sori medial, indusia glabrous or with a few short hairs.

Collections: Thwaites C.P. 714 (2 sheets), sub *Nephrodium molle* (PDA). Hillside above Potupitiya, Ratnapura District, in degraded forest, 450 m, 4 Dec. 1976, *Faden* 76/481 (K).

Rare.

Also in south-west India and the Seychelles.

Sphaerostephanos subtruncatus differs from *S. unitus* in its erect rhizome and softer, more deeply lobed, pinnae which are much less hairy beneath and without prominently raised veins. The Peradeniya examples agree closely with specimens from south-west India, save for their subglabrous stipes. The species appears not to have been re-collected in Ceylon until Faden's 1976 gathering; the label on his specimen states that only one plant was seen.

Holttum cites four collections from India, and Christensen one from the Seychelles. A specimen from India at Genève, received from Kew and named as *Nephrodium molle,* is another example of *Sphaerostephanos subtruncatus.* A third sheet of *Thwaites* C.P. 714 at Peradeniya is *Christella hispidula* (Decaisne) Holttum, as is a sheet bearing the same number at Kew. Three sheets of *Thwaites* C.P. 714 at P and others at CGE and BM all represent *C. dentata* (Forssk.) Brownsey & Jermy.

3. **Sphaerostephanos unitus** (L.) Holttum

in *Jl. S. Afr. Bot.* **40** : 165 (1974).—*Polypodium unitum* L., *Syst. Nat.* 10th ed., **2** : 1326 (1759), excl. syn. Type: no locality (LINN).—*Aspidium unitum* (L.) Swartz in *J. Bot. Göttingen* **1800** (2) : 32 (1801) *nomen tantum.* Sensu Thwaites, *Enum. Pl. Zeyl.* : 391 (1864), non Mettenius—*Dryopteris unita* (L.) Kuntze, *Rev. Gen. Pl.* **2** : 811 (1891).—*Cyclosorus unitus* (L.) Ching, in *Bull. Fan meml Inst. Biol.* (Bot.) **8** : 192 (1938). Holttum, *Rev. Fl. Malaya* **2** : 260, fig. 147 (1955).

Aspidium cucullatum Blume, *Enum. Pl. Jav.* : 151 (1828). Type: Java (L).—*Nephrodium cucullatum* (Blume) Bedd., *Ferns S. Ind.* : t.88 (1863). Baker in Hook. & Baker, *Syn. Fil.* : 290 (1867). Bedd., *Handb. Ferns Brit. Ind.* : 270, fig. 138 (1883)..

Rhizome wide-creeping, apical region covered with narrow, brown scales; *stipes* 30–50 cm long to lowest unreduced pinnae, scaly at the base elsewhere *villose* with short appressed hairs but becoming glabrescent with age; *rhachis densely hairy*; lamina 40–60 cm long, pinnate with 15–25 (30) pairs of pinnae excluding *several pairs of abruptly reduced, auricle-like lower pinnae,* apex of frond pinna-like; pinnae up to 15 cm long, 0·75–1·5 cm wide, apex acuminate, base broadly cuneate, *margins cut down about one third* into rounded, acute, cucullate lobes; *veins* 8–10 pairs per lobe, thick and *raised beneath,* 1–$1\frac{1}{2}$ pairs anastomosing the next two pairs running to the long hyaline sinus membrane; upper surfaces of pinnae glabrous save for the strigose-hairy costae, *lower surfaces* of costae, costules and veins rather *densely clothed with pale, stiff hairs,* the veins and lamina surface also *dotted with small spherical sessile orange or yellow glands; texture* of frond *subcoriaceous*; sori supramedial on the veins which are generally all soriferous; indusium firm, persistent, usually eglandular and more or less hairy; sporangia glandular.

Collections: Thwaites C.P. 973 (BM; CGE; K; P; PDA). Peradeniya, 24 May 1915, *Petch* (PDA). Kotmalee, 1847, *Fortescue* (CGE). Badulla, *Freeman* 263 (BM). Common at Kandy, *Mrs Chevalier* (BM). Same locality, 1854, no collector's name (CGE). Same locality, 1868, 1871, *Randall* in herb. Rawson 3220 (BM). Galle, woods, May 1860, *Dubuc* (E). Point de Galle, 1875, *Lischke* (P). Caltura, woods, May 1820, *Leschenault* (P). Hunnasgiriya, 900 m, 18 Jan. 1954, *Schmid* 954 (BM). Rajawaka, Ratnapura District, moist roadside bank, 460 m, 30 Dec. 1976, *Faden* 76/660 (K). Between Hakgala and Ambawela, roadside 1650 m, Dec. 1950, *Sledge* 716, 722 (BM). Pussalamankada, between Kandy and Maturata, open ground above stream, 540 m, 18 Jan. 1954, *Sledge* 982 (BM). Unlocalised: 1819, *Moon* (BM). *Ferguson* (PDA; US 816403).

Common on moist roadside banks and open ground near streams in the west and centre, up to 1650 m.

East Africa, Madagascar and Mascarene Islands, Seychelles, southern India, Assam and Burma to Vietnam, throughout Malesia to New Guinea and the Philippine Islands, New Caledonia, Fiji and Samoa.

XV. PRONEPHRIUM Presl

Epimel. Bot. : 258 (1851). Holttum in *Blumea* **19** : 34 (1971); **20** : 105 (1972).

Caudex suberect to long-creeping; fronds simply pinnate (rarely simple) with subentire pinnae and terminal pinna-like segment, the basal pinnae not reduced; most pairs of veins anastomosing to form united excurrent vein between costules; lower surface of pinnae often pustular when dry, acicular or hooked hairs frequent on one or both surfaces; sori indusiate, or exindusiate and then spreading along veins, sporangia often bearing hairs or glands near annulus; spores with a continuous wing and a few cross-wings. n = 36.

About 60 species; India and Ceylon, southern China southwards throughout Malesia; north-eastern Australia and the Pacific Islands.

Holttum (*loc. cit.*) divided this genus into three Sections. The smallest of these, Sect. *Grypothrix* Holttum, is distinguished by the presence of hooked hairs on the pinnae and sporangia; two of the four Ceylonese species of *Pronephrium* belong to this group. They are widely different in appearance from the other two species which belong to the two other generic Sections.

1. **Pronephrium articulatum** (Houlst. & Moore) Holttum

in *Blumea* **20** : 116 (1972).—*Nephrodium articulatum* Houlst. & Moore, *Gdnrs' Mag. Bot. Hort. Flor. Nat. Sci.* : 293 (1851). Type: cult. Hort. Bot. Kew ex Ceylon, 1845, *Gardner* 1104 bis (BM; CGE; K).—*Aspidium articulatum* (Houlst. & Moore) Lowe, *Ferns Brit. & Exot.* **6** : t.49 (1857), non Swartz (1801).

Nephrodium abruptum sensu Hook., *Spec. Fil.* **4** : 77–78, t.241B (1862) p.p., non *Aspidium abruptum* Blume (1828). Bedd., *Ferns S. Ind.* : 31, t.86 (1863), non *Aspidium abruptum* Blume.—*Aspidium abruptum* sensu Thwaites, *Enum. Pl. Zeyl.* : 391 (1864), non Blume (1828).

Nephrodium pennigerum Baker in Hook. & Baker, *Syn. Fil.* 2 ed. : 292 (1874) p.p. C. B. Clarke in *Trans. Linn. Soc.* (Bot.) II, **1** : 532 (1880), quoad plantae Zeylanicae. Bedd., *Handb. Ferns Brit. Ind.* : 277 (1883) p.p.; *Handb. Suppl.* : 73 (1892).

Nephrodium glandulosum var. *laete-strigosum* C. B. Clarke in *Trans. Linn. Soc.* (Bot.) II, **1** : 532, t.74 fig. 2 (1880). Type: [Bangladesh,] Chittagong, *Clarke* 19900 (K).

Dryopteris megaphylla (Mettenius) Christensen, *Index Fil.* : 277 (1906) p.p. quoad plantae Zeylanicae.

Dryopteris indica van Rosenb., *Malay. Ferns* : 224 (1909).

Cyclosorus laete-strigosus (Clarke) Ching in *Bull. Fan meml Inst. Biol.* (Bot.) **8** : 227 (1938).

Rhizome short-creeping, stipes up to 50 cm long, sometimes longer, with scattered broad thin brown scales especially in the lower part and sparsely hairy throughout as is the rhachis; lamina 50–80 (100) cm, pinnate with up to 20 pairs of patent pinnae below the terminal pinna; *lower pinnae not reduced*, largest pinnae up to 20 × 3 cm apex acuminate, base of upper ones truncate to broadly cuneate, lower ones more narrowly cuneate, margins shallowly lobed to about $\frac{1}{4}$ way to the costa, the lobes rounded or subacute; veins up to 12 pairs about 3–5 pairs anastomosing the next 2–3 running into the sinus membrane, veins in the terminal pinna often forking and anastomosing; *costae and veins sparsely appressed-hairy above and beneath* with short stiff hairs on the lamina surface (sometimes rather plentiful on the upper surface), the *lower surface with scattered small, sessile ochre-coloured glands* on and between the veins; fertile fronds contracted with narrowed pinnae; texture herbaceous; sori medial, indusia glabrous; spores spinulose.

Collections: Thwaites C.P. 3271 (BM; CGE; K; P; PDA: Haldingmulle, April 1856; Wattegodde 1856). Hantane range, in forests, Aug. 1844, *Gardner* 1104 (bis) (BM; CGE). Lady Horton's Walk, Kandy, in forest, 600 m, Feb., March 1954, *Sledge* 1144, 1363 (BM). Unlocalised: 1884, *Wall* (PDA). *W. Robinson* C. 155 (K).

Forests of Central Province from 600–1200 m.
Also in India, Bangladesh, Burma, northern Thailand and western China.

Holttum's description refers to the rootstock as being erect though Houlston & Moore's (*loc. cit.*) original description, described from cultivated plants at Kew, alludes to a 'thick creeping rhizome.' Beddome's description in the *Handbook* states 'caudex erect', but this is corrected in the *Supplement* to 'often, if not always, more or less creeping.' My no. 1363 has a creeping rhizome, though this is not evident in my no. 1144.

This species was described from Ceylonese plants first found by Gardner in 1844 and sent to Kew by him in 1845. It has probably been a rather rare species confined to forests at a moderate elevation in the Central Province, and since these have mostly now been cleared for plantations, it will certainly be rarer now. My collections from Kandy are the only recent gatherings.

2. **Pronephrium gardneri** Holttum

in *Kew Bull.* **26** : 81 (1971). Type: Ceylon, *Gardner* 1137 (K, holotype). [non *Gardner* 1135, Holttum *loc. cit.]*
3063 (K)].—*Nephrodium urophyllum* sensu Bedd., *Ferns S. India Suppl.* : 18 (1876); *Handb. Ferns Brit. Ind.* : 274 (1883) p.p.
Polypodium granulosum sensu Thwaites, *Enum. Pl. Zeyl.* : 394 (1864) p.p., non Presl.

Stipes 50 cm or more long, stramineous, glabrous save in the groove. Fronds 70 cm or more long with 10–12 pairs of pinnae, the lowermost up to 25 × 3·5 (4) cm, narrowly oblong, shortly acuminate at the apex, base truncate or broadly cuneate (save the lower ones which are narrowed towards the base), margins coarsely crenate, shortly ciliate; costules 4·5–5·5 mm apart; veins 10–11 pairs, slender, slightly raised, 7 pairs anastomosing (the excurrent nerves often free in lower parts), two pairs joining the sinus membrane, three or four veins reaching the margin. Lower surface of rhachis glabrous, of the costae minutely pilose, lamina minutely pustulose; upper surface of rhachis and costae shortly pilose. Sori medial, round, exindusiate; sporangia smooth, spores with a translucent wing with minutely erose margin and a few transverse wings.

Collections: Hantane Range, in forests, Aug. 1844, *Gardner* 1137 (CGE; K, holotype). *Thwaites* C.P. 3063 (P; PDA: Hantane, Jan. 1854). *Thwaites* C.P. 3063 (K).

Forest near Kandy.
Endemic to Ceylon.

Thwaites was surely wrong in stating that this fern was 'not uncommon' in the forests of the Central Province. Very few collections exist (only five sheets having been located) and all are from the vicinity of Oodawella in the Hantane range near Kandy. No forest now remains on these hills, and since no specimens have been found elsewhere, it is probable that this species is extinct.

3. **Pronephrium triphyllum** (Swartz) Holttum

in *Blumea* **20** : 122 (1972).—*Meniscium triphyllum* Swartz in *J. Bot. Göttingen* **1800** (2) : 16 (1801); Hook & Baker *Syn. Fil.* 2nd ed. : 391 (1874). Bedd., *Handb. Ferns Brit Ind.* : 397, t.231 (1883). Type: No locality or collector (S–PA).—*Abacopteris triphylla* (Swartz) Ching in *Bull. Fan meml. Inst. Biol.* (Bot.) **8** : 241 (1938).

Rhizome long-creeping, clothed near the apex with linear, brown, ciliate scales; stipes sulcate, hairy, 30 cm or more long in fertile fronds, sterile fronds with shorter stipes; *lamina trifoliate or with five pinnae*, the *terminal pinna largest, oblong-lanceolate*, apex acute or acuminate, base rounded, *margins entire* or sinuate, glabrous above save on the costa, with hooked hairs on the costa and veins beneath; texture herbaceous; terminal pinna of sterile fronds up to 15 cm long, 2–3½ cm broad, of fertile fronds usually narrower; veins normally 8–10 pairs anastomosing at a wide angle, the excurrent vein often free though usually united to the next pair of veins above, in the fertile pinnae the veins almost at right angles to the costules, the exindusiate sori occupying almost the whole length of the veins; *sporangia setose with hooked hairs*, spores spinulose.

Collections: Thwaites C.P. 1293 (CGE; K; P; PDA: Pasdun Korle, Dec. 1845, *Gardner*; Ambagamuwa, Nov. 1854; Hunnasgiriya, April 1857). Pussilawa, 1847, *E. Tennents* (CGE), *Ferguson* (PDA). By track from Palawatta to Pahale Hewissa, on sandy ground in shade, 45 m, 20 Jan. 1951, *Sledge* 886 (BM). Gongalla Hill, ± 1000 m, 11 March 1954, *Sledge* 1261 (BM). Near Hiniduma, Southern Province, shady bank by path, 3 April 1954, *Sledge* 1393 (BM).

Damp, shady places at low to moderate elevations.

India, Ceylon, Burma, Thailand, Malaysia, China, Japan, Taiwan, the Philippine Islands and Australia (Queensland).

Beddome's *Meniscium parishii*, described from Burma, has four or five pairs of free pinnae beneath the terminal pinna. A specimen of Griffith's from north-east India has six pairs. Beddome reduced his species to a variety of *M. triphyllum* in his *Handbook* and Holttum also treated it as a variety in his *Ferns of Malaya*. However, in his account of the genus *Pronephrium*, Holttum (*Blumea, loc. cit.*) raises *parishii* to specific rank and alters the circumscription to include all plants with more than one pair of pinnae, thus including Ceylon in its distribution. Yet fully mature fertile fronds bearing three or five pinnae may be found attached to the same rhizome. It is also improbable that if populations of plants with five pinnae existed in Ceylon that these would have been overlooked by collectors. I have seen no specimens from Ceylon which match Beddome's illustration (*Ferns Brit. Ind.* t.184 (1866)) of his *Meniscium parishii*. Whatever the status of plants from Burma and northern India, I see no grounds for the recognition, even at varietal level, of another taxon from Ceylon.

4. **Pronephrium thwaitesii** (Hook.) Holttum

in *Blumea* **20** : 122 (1972).—*Meniscium thwaitesii* Hook., *Fil. Exot.* sub t.83 (1859). Thwaites, *Enum. Pl. Zeyl.* : 382 (1864). Bedd., *Handb. Ferns Brit. Ind.* : 399, fig. 232 (1883). Type: Ceylon, *Thwaites* C.P. 3145 (K).—*Abacopteris thwaitesii* (Hook.) Ching in *Bull. Fan meml Inst. Biol.* (Bot.) **8** : 243 (1938).

Rhizome wide-creeping; stipes up to 30 cm long, nearly naked save at the base; rhachis hairy; lamina subdeltoid in outline 15–25 × 10–15 cm, *pinnate with 2–4 pairs of free pinnae beneath the apical pinna which is pinnate below with adnate segments,* becoming pinnatifid then lobed then crenate distally. Lowest pair of pinnae the largest, 5–10 × 1–1½ cm, subsessile or shortly stalked, apex acuminate, margins crenate or shallowly lobed, divisions of the apical pinna entire, narrower and blunter and often falcately curved; surface of pinnae glabrous above save on the costa, hairy with hooked hairs on the veins beneath, areoles 4–5 in the lower pinnae between the costa and margin; sori exindusiate, those on lower veins elongate, on distal veins circular; *sporangia setose with hooked hairs.*

Collection: Thwaites C.P. 3145 (CGE; K, holotype; P; PDA).

Forests of Central Province from 900–1200 m.
Also in southern India (Nilgiris Hills).

Information given on the three sheets in PDA indicates that *Pronephrium thwaitesii* has been collected in a small number of widely separated localities in the Central Province, viz. Udapusselawa (April 1854), Bogawantalawa (Nov. 1855) and at Kotagalla and Lagalla in Matale East. No collections have been made however in the last 100 years, either in Ceylon or southern India.

Holttum (*loc. cit.*) has suggested that this is 'probably a hybrid between *P. triphyllum* and a species with lobed pinnae.' Elsewhere he (*Blumea* **19** : 36 (1971)) suggested *Trigonospora ciliata* as the other possible parent. I see more to refute than to support this suggestion. No station is known in which *Pronephrium triphyllum* and *P. thwaitesii* occur together. The second parent could scarcely be either *P. articulatum* or *P. gardneri,* neither of which has ever been collected in any of the areas from which *P. thwaitesii* has been recorded. If hybridisation involved a more distantly related species belonging to another thelypteroid group, as is implied by Holttum, this would probably be reflected in spore sterility and malformed sporangia; yet the sporangia and spores are well formed in the specimens I have examined.

Wall (*Cat. Ceylon Ferns,* notes : 7 (1873)) was the first to recognise that the entire-margined, blunt-ended and falcately-curved distal 'pinnae' really belong to the apical pinna, and represent its lower, fully pinnated portion, the only true pinnae being the 2–4 pairs of stalked, crenate-margined and acuminate basal pairs. He also records the important field observation that in East Matale (the only region in which *Pronephrium triphyllum* is known to occur in the same area as *P. thwaitesii*) 'the least divided forms of *M. Thwaitesii* are found . . . on the same range of mountains, but on the opposite side of the range, where the most divided forms of *M. Triphyllum* grow.' The inference is that the boundaries between *P. triphyllum, P. parishii* and *P. thwaitesii* may be less clearly defined than has been supposed. The relationships between the three taxa need reinvestigation in the field rather than the herbarium.

[**Pronephrium nudatum** (Roxb.) Holttum in *Blumea* **20** : 111 (1972) (*Nephrodium moulmeinense* Bedd., *Handb. Ferns Brit. Ind.* : 275 (1883)) is not a Ceylon fern. Single specimens at CGE, K & PDA from Ceylon were doubtless of botanical garden origin.]

XVI. STEGNOGRAMMA Blume

Enum. Pl. Jav. : 172 (1828) emend. K. Iwats. in *Acta phytotax. geobot. Kyoto* **19** : 112–126 (1963).

Caudex ascending or short-creeping; stipe and rhachis hairy with unicellular or septate hairs; fronds pinnate with subentire or pinnatifid pinnae, the basal pinnae not or little reduced, the upper ones coadnate at base; aerophores lacking; veins free or with goniopteroid anastomosis; surfaces of pinnae hairy, lacking spherical glands; sori exindusiate, elongated along the veins, sporangia setose; spores finely spinulose or with many small wings. n = 36.

About 12 species, from Spain, Macaronesia, tropical and southern Africa eastwards across the warmer parts of east Asia to Japan and south to the Philippine Islands and Indonesia; a few in tropical America.

1. **Stegnogramma pozoi** (Lag.) K. Iwats. var. **petiolata** (Ching) Sledge, **stat. nov.**

Leptogramma petiolata Ching in *Acta phytotax. sin.* **8** : 319 (1963). Type: Ceylon, *G. Wall.*

Grammitis totta sensu Thwaites, *Enum. Pl. Zeyl.* : 382 (1864), non Presl.—*Leptogramme totta* sensu Bedd., *Handb. Ferns Brit. Ind.* : 377 p.p. excl. fig. 215 (1883).

Rhizome short-creeping clothed with lanceolate, brown, ciliate scales. Fronds 20–60 cm, stipe shorter than lamina bearing scattered brown scales below and a *mixture of long and short, spreading, white, acicular hairs throughout*; rhachis similarly hairy. *Lamina lanceolate to narrowly oblong-lanceolate,* 4–15 cm wide, pinnate with *up to 9 pairs of free pinnae* below the broadly adnate distal ones, *several pairs of lower pinnae subsessile or very shortly stalked,* the lowermost pair sometimes reduced. Pinnae 2–6 (10) × 1–1·75 cm, truncate at the base and usually rather suddenly narrowed to a blunt or subacute apex, rarely attenuate, lobed less than half way to the costa with the lobes blunt and rounded or only crenate-lobate in small fronds, bearing a mixture of some long and many short hairs on the costa and veins on both surfaces and often minute hairs on the lamina surface; veins in the segments simple, free or rarely with occasional anastomoses; texture herbaceous. *Sori linear, medial, exindusiate* with setose sporangia.

Collections: Thwaites C.P. 1292 (BM; CGE; K; P). Newara Eliya, in woods, 1800 m, Sept. 1844, *Gardner* 1071 (BM; CGE; P). Same locality: April 1899, *Gamble* 27567 (K). Moon Plains near Newara Eliya, 1800 m, 23 Dec. 1950, *Ballard* 1201 (K). By track from Pattipola to Horton Plains, 1800 m, 20 Dec. 1950, *Sledge* 667 (BM), Horton Plains, by stream in shady gully, 2040 m, 19 Dec. 1950, *Sledge* 687 (BM). Horton Plains, 2070 m, March 1954, *Schmid* 1397 (BM). Same locality, on roadside banks in forest, *c.*2090 m, 15 Nov. 1976, *Faden* 76/285 (K). Ramboda Pass-Maturata track, in shady forest, 1940 m, 17 March 1954, *Sledge* 1305, 1316 (BM). Hakgala, 1800 m, 20 March 1954, *Sledge* 1340 (BM). Unlocalised: *Walker* (K). *Bradford* 481 (P). May 1906, *Matthew* (K). *Mrs Chevalier* (BM). *Freeman* 334A, 335B, 336C (BM).

In forests about Newara Eliya, above 1750 m.

Stegnogramma pozoi s. lat. is recorded from Spain, Madeira & west Africa to China and Japan; var. *petiolata* from Ceylon and Java.

Ching's description of *Leptogramma petiolata* is based on two collections from Ceylon; the type is said to be based on a collection by 'Wallich' and the other gathering is cited as *Thwaites* 481. The former is an error for G. Wall; the latter presumably refers to *Bradford* 481 of which there are three sheets from Ceylon in P. *Thwaites* C.P. 481 is a species of *Viscum.* Although Ching's description appears to be based on only two sheets, more ample material confirms that Ceylon plants differ from south Indian plants in their generally smaller stature, their shorter (3–4 cm) pinnae, which are proportionately broader and more abruptly narrowed into a blunt or subacute apex (rarely acuminate as described by Ching), and in having many pairs of pinnae free from the rhachis and shortly stalked—not 'longe petiolatis.' South Indian plants have pinnae 6–12 cm long, more gradually narrowed at their apices and either all are adnate to the axis, or at most the lower 2–3 pairs are free but sessile. The common Ceylon form therefore is distinctive in appearance and matches specimens from Java, which also have shortly petiolate lower pinnae, more satisfactorily than those from southern India. Not all specimens, however, agree in being small with short pinnae; *Sledge* 1305 resembles the Indian form in possessing pinnae 6–10 cm long and some other Ceylon specimens in herbaria (e.g. *Schmid* 1397 in BM) show an overlap in size and frond outline, though such fronds still differ from south Indian ones in having numerous pairs of free, shortly stalked pinnae. Specimens from Sikkim and Assam do not appear to be significantly different from those from south India.

Shortly before Ching described *Leptogramma petiolata,* Iwatsuki (in *Acta phytotax. geobot. Kyoto* **19** : 112–126 (1963)) published a revision of *Stegnogramma,* wherein *Leptogramma* is treated as a section. A consideration of the range of variation of the predominantly African *S. pozoi* and the Asiatic *Leptogramma mollissima* (Kunze) Ching led Iwatsuki to reject specific separation, but he maintained them as geographical subspecies and commented upon the distinctive appearance of Ceylon plants, which he considered to be intermediate between the two.

Gymnogramma totta var. *mollissima* Kunze with which Ching had earlier identified Ceylon plants (as *Leptogramma mollissima* (Kunze) Ching), was described from the Nilgiri hills. The specimens cited by Kunze are presumed to be at Berlin but Meyer informs me that he has been unable to find them. It is doubtful if Iwatsuki is correct in identifying plants from China and Japan as *Stegnogramma pozoi subsp. mollissima,* since these have deeply lobed pinnae with the lowest pair often much elongated. They do not match plants from northern India or Ceylon and may well represent another taxon. A satisfactory treatment however of *S. pozoi sensu lato* cannot be based on herbarium material alone, since boundaries between described taxa are too ill-defined. This applies to African as well as to Asiatic plants; some specimens from eastern and southern Africa are nearer to Indian than to West African plants, or to specimens from Spain whence *Hemionitis pozoi* Lagasca was first described. Until experimental work affords a firmer foundation for the systematic treatment of the group, I believe varietal names should preferably be substituted for those of species. The taxon first described from the Nilgiri Hills then becomes **Stegnogramma pozoi** var. **mollissima** (Kunze) Sledge, **comb. nov.** (*Gymnogramma totta* var. *mollissima* Kunze in *Linnaea* **24** : 249 (1851)). Cytological information is at present limited to chromosome counts on plants from Madeira and Ceylon which have shown that the former is tetraploid and the latter diploid.

Both Ching (*loc. cit.*) and Pichi-Sermolli (*Webbia,* **31** : 445 (1977)) maintain *Leptogramma, Stegnogramma* and *Dictyocline.* Iwatsuki (*loc. cit.*) and Holttum (*Blumea* **19** : 38 (1971)) combine them as a single genus, *Stegnogramma.* The principal distinction between *Leptogramma* and *Stegnogramma* lies in their free and anastomosing veins respectively, but this difference is regarded here as inconstant. In specimens of the Ceylon species the basal acroscopic and basiscopic veins of adjacent lobes arch outwards and either reach the sinus separately or become contiguous, though not confluent, at its base. Sometimes the veins meet below the sinus and then they either remain contiguous but separate from one another, or they may fuse. Such fusions, however, if present at all, are normally so infrequent that the fronds are properly described as free-veined. Yet, occasionally in Ceylon plants, casual and irregular vein fusions may be rather numerous. A specimen of *Gardner* 1292 in Herb. Hooker at K shows such frequent anastomoses that it has been misidentified both as *S. aspidioides* Blume and *S. asplenioides* J.Sm. ex Ching. In one of my own gatherings (*Sledge* 1340) fusions are also rather plentiful. Ching's *Leptogramma himalaica,* which Iwatsuki has upheld, was evidently based on another such deviation from type, for, apart from occasional vein fusions, all the other characters attributed to it fall within the range of variation of var. *mollissima.* Morton (*Am. Fern. J.* **56** : 179 (1966)) reduced *L. himalaica,* to a subspecies of *Thelypteris pozoi,* but I believe that it is only a form. In all such plants the fusion lack the regularity which characterises the sections *Stegnogramma* and *Haplogramma.* A parallel, but reversed example, of a free-veined species within the subgoniopteroid-veined section *Haplogramma,* is provided by *S. leptogrammoides* K. Iwats. wherein most veins are free but casual and irregular fusions are frequent. Such examples vindicate Iwatsuki's rejection of free, versus fusing, veins as a basis for generic separation within the group.

There is a sheet of *Stegnogramma asplenioides* J.Sm. ex Ching in Herb. Hooker at K purporting to have come from Ceylon annotated 'H.f. & T.' and originally identified by Hooker and published (in *Sp. Fil.* **5** : 150 (1864)) as *S. aspidioides* Blume. The specimens, two fronds, are inseparable from another Hooker *filius* & Thomson sheet from the Khasia Hills, and since Hooker & Thomson did not collect in Ceylon and no subsequent collector has found *S. asplenioides* there, it is more likely that both sheets came from Assam. This sheet is the source of the erroneous records for *S. aspidioides* from Ceylon in the *Species Filicum* and *Synopsis Filicum.* Thwaites, Trimen, Beddome, Willis, Ferguson, and Wall, all either dismissed it as an error or placed the record in brackets in their works as being apocryphal. When Ching again cited it from Ceylon he was evidently copying from Hooker, and Iwatsuki, who has also wrongly included Ceylon in the distribution of *S. aspidioides,* appears to have copied from Ching.

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Studies in the genus *Hypericum* L. (Guttiferae)
2. Characters of the genus

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Synopsis

After a review of the relationships of *Hypericum* and a discussion of research methods and evolutionary diagrams employed, a detailed account is given of morphological variation in *Hypericum*, from habit to seed. This is followed by a summary by Dr G. C. S. Clarke of the variation in pollen structure, which is treated in detail elsewhere, and a discussion of flower and fruit biology (pollination, breeding systems, seed dispersal) in the genus. An account of development from embryo to flower is then given. A detailed discussion of floral vasculature in *Hypericum* shows how variation in this character parallels and helps to explain morphological variation in the flower.

An outline of the distribution (systematic and anatomical) of the secretory system and its contents in *Hypericum* and the Hypericoideae indicates that the occurrence of hypericin and pseudo-hypericin has a limited but important taxonomic value. An account of variation in *Hypericum* chromosomes, including what is believed to be a complete list of known chromosome numbers in the genus, is followed by a consideration of hybridization in the genus. Finally, the distribution of *Hypericum* and allied genera is discussed and interpreted with recourse to the theory of plate tectonics.

One species originally described in *Hypericum* (*H. steyermarkii* Standley) is transferred to *Santomasia* **gen. nov.**, on account mainly of the presence in its flowers of antisepalous fasciclodes (sterile stamen-fascicles). One species (*H. concinnum* Bentham) is transferred from sect. *Hypericum* to sect. *Concinna* **sect. nov.** The pentaploid form of the hybrid *H. maculatum* Crantz x *perforatum* L. is designated as a nothomorph, *H.* x *desetangsii* Lamotte nm. *perforatiforme* (Fröhl.) N. Robson **comb. et stat. nov.**; and the variegated form of *H.* x *moseranum* Luquet ex André is also given the rank of nothomorph, as nm. *tricolor* (Maumené) N. Robson **stat. nov.**

1. Introduction

The genus *Hypericum* having been circumscribed and subdivided in the first paper of this series (Robson, 1977*a*), this contribution is concerned mainly with the characters of the whole genus and its overall variation and distribution. Further papers will treat each section individually, and a final one will, it is hoped, provide an extended summary and include any necessary amendments. First, however, it is necessary to discuss the status of the anomalous *H. steyermarkii* Standley (cf. Robson, 1977*a* : 316) and how it affects the classification of the Guttiferae.

Relationships of *Hypericum*—further considerations

(*a*) *Delimitation of the genus*

When Standley (1940) described *Hypericum steyermarkii*, based on a collection from Volcán de Santo Tomás in Guatemala (*Steyermark* 34760), he remarked that it had no close allies in either Mexico or Central America. A superficial study of the type and another

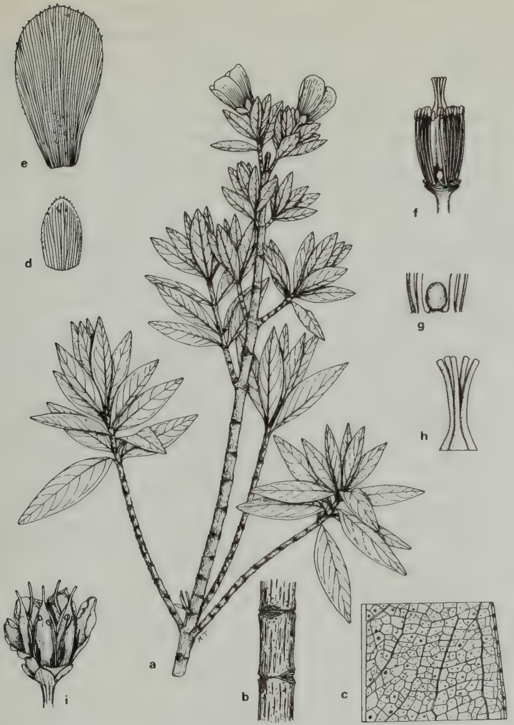

Fig. 1 *Santomasia steyermarkii:* (a) habit (x 0·5); (b) stem nodes and leaf scars (x 1); (c) section of leaf, showing venation and glands (x 2·5); (d) sepal (x 2·5); (e) petal (x 1·5); (f) flower with perianth removed (x 1); (g) fasciclode and adjacent stamens (x 2); (h) styles (x 2); (i) flower with dehiscent capsule (one petal cut) (x 1) (a–c, *Matuda* 2894; d–i, *Steyermark* 34760).

collection (*Matuda* 2894, from Volcán Tacana West, Mexico) showed their undoubted resemblance to members of *Hypericum* sect. *Campylosporus*; but it was not until the first paper was in an advanced stage of preparation that a detailed examination of these specimens revealed that *H. steyermarkii* could not be retained in *Hypericum*.

The first anomalous character to be observed was the presence of vestigial staminodes between the stamen fascicles (Fig. 1f, g), and subsequently it was realised that the leaf venation and the occasional umbellate inflorescence were also not to be matched in *Hypericum*. In addition, *H. steyermarkii* has fascicles of only 11–12 stamens, petals that are apparently erect in flower, and often markedly auriculate leaf-bases. The last two characters suggest a relationship with *H. bequaertii**, the most unspecialised species in *Hypericum* (Robson, 1979); but other characters, e.g. the stamen number, do not fit into the pattern of

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*Authorities for names of *Hypericum* taxa will not normally be cited unless they differ from those in Robson (1977*a*) or are additional to them.

variation in sect *Campylosporus*. In sum, therefore (i) *H. steyermarkii* is less specialised than other species of *Hypericum* in retaining remnants of the antisepalous androecial whorl; but (ii) it has certain characters that are more specialised than those of the most primitive *Hypericum* species and would therefore appear to have evolved along a different evolutionary line from them.

In Table 1 some characters of *H. steyermarkii* are compared with corresponding ones of *H. bequaertii* and also of *H. styphelioides*, the most primitive species of sect. 29. *Brathys*. The primitive condition has been marked for each character in which it has been ascertained, and a study of these marked characters shows that no one species is completely unspecialised relative to the others.

Table 1 Characters of *Hypericum steyermarkii* compared with those of *H. bequaertii* and *H. styphelioides* (Belize form)

	H. steyermarkii	*H. bequaertii*	*H. styphelioides*
Leaves	elliptic (1: b = c.3)	± narrowly elliptic to narrowly oblong (1: b = 5–8)	narrowly oblong (1: b = 4–5)
Leaf-base	angustate, reflexed-auriculate	cuneate*, reflexed-auriculate	cuneate*, not reflexed-auriculate
Leaf-venation	pinnate (oblique), densely reticulate	parallel*, not reticulate*	parallel*, not reticulate*
Dark glands on leaves	present, marginal and laminar	absent*	absent*
Pellucid glands on leaves	punctiform	linear and punctiform*	punctiform
Inflorescence	1(2–4)-flowered (umbellate if more than one)	1-flowered	1-flowered
Dark glands on sepals	present, marginal and submarginal	absent or present, marginal and inframarginal	absent
Petals	erect*, subsymmetrical*, without lateral apiculus*	erect*, asymmetrical, with rounded lateral apiculus	spreading, asymmetrical, with acute lateral apiculus
Stamens per fascicle	11–12	c.30*	c.50*
Staminodes	present*	absent	absent
Styles	free*	c.3/4 coherent	free*
Seed	shallowly carinate with apical wing	not carinate or winged	slightly carinate, not winged

* = primitive state of character

Although the inflorescence of *H. steyermarkii* is usually a single flower with bracteoles at the base of the pedicel, in the type specimen it is sometimes 2–4-flowered. In such inflorescences the bracteoles are crowded together, i.e. the inflorescence is umbellate, a state that is otherwise unknown in primitive species of *Hypericum*. The leaf of *H. steyermarkii*, broad but narrowing to a sessile reflexed-auriculate base, contrasts with those of species of *Hypericum* proper, where the only species in which such leaf-bases are at all strongly developed are the most primitive species of the most primitive section, *Campylosporus* (*H.*

bequaertii, H. revolutum and *H. lanceolatum*). In these species, however, the leaf is narrow, and the functional secondary veins are much fewer than they are in the leaf of *H. steyermarkii* (cf. Fig. 9d, e) (p. 77). These secondary veins and the intervening glandular canals are almost parallel with the leaf margin, as are those towards the base of the leaves of two Bonnetiaceous genera, *Neblinaria* and *Neogleasonia*, recently described by Maguire (1972) (Fig. 9a, b). Melville (1969) described the leaf-venation of some specimens of *H. bequaertii* (subparallel veins from a pedate base) as gangamopteroid, a state which he regards as primitive in the Angiosperms and as having given rise to the glossopteroid (pinnate) state. According to his later terminology of leaf architecture (Melville, 1976), such venation is pedati-flabellate (cf. *H. styphelioides,* Fig. 9f); whereas the venation of the above-mentioned Bonnetiaceous genera is lirate, an early stage of the more advanced pinnate system. On the other hand, whereas in *Hypericum* the leaf always has a complete midrib, in *Neblinaria*, the midrib is well-developed only at the base, a very primitive state (Fig. 9a). In contrast to Melville, Hickey & Wolfe (1975) regard pinnate venation as probably primitive in the Dicotyledons and would describe the venation of *H. bequaertii* as parallelodromous (Hickey, 1973), that of *Neblinaria* and *Neogleasonia* (Fig. 9b) being craspedodromous and thus in their view more primitive.

The evolutionary trends in the leaf venation of the Bonnetiaceae-Guttiferae suggest that Melville is right and that the flabellate type of venation has given rise first to the lirate type and then to more typical pinnate types. In this sequence the major venation of *H. steyermarkii* is at least partly pinnate, approaching that of, say, *Bonnetia*. More advanced species of *Hypericum* proper also have pinnate leaf-venation, but this has evolved in a different way (see below, p. 80). A further difference occurs in the densely reticulate tertiary venation in *H. steyermarkii*, which is an advanced character comparable with, but quite different in origin from, the vein-reticulations in *H. roeperanum* and *H. gnidiifolium*, relatively advanced members of sect. 1. *Campylosporus* (cf. Robson, 1979).

The dark gland dots in the leaves and sepals of *H. steyermarkii* (Figs 1c, d, 9d) are comparable with those of *H. bequaertii* (Fig. 9c), although the laminar ones recall the more superficial (less deeply immersed) glands of some Bonnetiaceous genera (e.g. *Bonnetia*). On the other hand, the numerous pellucid gland dots appear to be homologous with the minute ventral pellucid gland dots of *H. bequaertii* and with those of *H. styphelioides* (Fig. 9f), not with the scattered pellucid gland dots in the vein areoli of e.g. *H. roeperanum*. These originate from functionless veins, as will be shown later.

With two isolated localities in Central America, *H. steyermarkii* has a quite different distribution from that of sect. *Campylosporus*, which is confined to the African mainland and some adjacent islands. Although sect. *Brathys* is Central and South American, *H. styphelioides* and its other species are even less similar to the Mexico–Guatemalan plant. Despite all these differences, *H. steyermarkii* is in general much more closely related to *Hypericum* proper than it is to any other genera. Its appropriate position would therefore seem to be as a second genus of the Hypericeae cognate with *Hypericum*. The new genus is named *Santomasia* after the type locality in Guatemala, Volcán Santo Tomás.

Santomasia N. Robson, **gen. nov.**

Hyperico L. affine, a quo staminorum fasciculis sterilibus reductis 5 inter eos fertiles insertis, inflorescentia 1-florata vel fasciculata, differt.

Arbores vel frutices glabri. Folia opposita integra exstipulata penninerva glandulis pellucidis nigricantibusque obsita. *Inflorescentia* terminalis, 1-florata vel 2–4-florata fasciculata. *Sepala* 5, quincuncialia glandulis pellucidis nigricantibusque obsita. *Petala* lutea subsymmetrica erecta post anthesin persistentia. *Staminorum fasciculi* 5, filamentis basi breve coalitis anthera glandulifera ferentibus, post anthesin persistentia. *Staminodia* (staminorum fasciculi steriles) 5, parva, inter staminorum fasciculos fertiles inserta. *Ovarium* 5-loculare loculis ∞-ovulatis, stylis elongatis liberis stigmatibus parvis. *Fructus* capsularis valvis longitudinaliter anguste vittatis, ab apice dehiscentibus. *Semina* numerosa, cylindrica vade carinata, terminale alato-appendiculata. *Grana pollinis* tricolporata sphaeroidalia, colpis longislatis, endoaperturis lalongatis, ornamentatione microreticulati, munita.

TYPUS GENERIS: *S. steyermarkii* (Standley) N. Robson
Genus adhuc monospecificum.

S. steyermarkii (Standley) N. Robson, **comb. nov.**

Hypericum steyermarkii Standley in *Publs Field Mus. nat. Hist. Chicago* (Bot.) **22** : 160 (1940); Standley & Williams in *Fieldiana* (Bot.) **24** (7) : 50 (1961).

Shrub or tree 2–9 m high, much branched, with branches ascending; bark grey, fissured. *Stem* 4-lined, slightly flattened and orange-brown when young, soon 2-lined to terete with rather swollen nodes; internodes 4–15 mm long, much shorter than the leaves, with numerous small reddish or dark glands. *Leaves* sessile; lamina 25–70 × 9–24 mm, elliptic, acute or apiculate, the margin plane, the base cuneate to angustate or reflexed-auriculate, paler beneath, not glaucous, chartaceous, the lower ones soon deciduous, with 9–14 lateral veins, the lower ones arcuate, the middle ones spreading, the upper ones flexuous and ascending, and a uniform densely reticulate tertiary venation, the laminar glands very small, punctiform, pellucid and sometimes also dark, the inframarginal gland-dots pale, dense, alternating with more widely spaced dark dots. *Inflorescence* 1–4-flowered; pedicel 9–20 mm long, sometimes dark-gland-dotted; bracts foliar but smaller and broader; flowers *c.* 3–4 mm in diam., erect. *Sepals* free, imbricate, equal, reflexed in fruit, 4–7 × 2·5–3 mm, broadly ovate, acute to obtuse, with margin entire or eroded-glandular-ciliate towards the apex, with midrib obscure; laminar glands pellucid, numerous, linear, submarginal gland-dots dark, a few subapical, the rest dispersed; marginal dark glands few, present especially towards the apex, sessile or on cilia. *Petals* deep yellow, 17–21 × 9–11 mm, *c.* 4–4·5 × as long as the sepals, obovate, without lateral apiculus, the margin distally dark-glandular-ciliate, sometimes with a few large submarginal dark glands, with pellucid linear glands interrupted distally, erect at anthesis, persistent in fruit. *Stamen fascicles c.* 10 mm long, *c.* 0·5 × as long as the petals, each with 11–12 stamens, persistent in fruit; filaments shortly united, relatively stout (cf. *Hypericum*); anther gland amber. *Staminodial fascicles c.* 1·5 mm long, oblong, truncate, spreading, fleshy. *Ovary c.* 8 × 3 mm, narrowly ovoid; styles 3·5–4 mm long, erect to near apex. *Capsule* 12–14 × 10 mm, ovoid-cylindric, with valves finely longitudinally vittate. Seeds pale brown, cylindric, *c.* 2–2·5 mm long, shallowly carinate, with terminal winged appendage, finely shallowly linear-reticulate.

HABITAT. 'In forest of pine and *Abies*', 2500–3700 m.

DISTRIBUTION. Guatemala (Quezaltenango) and Mexico (Chiapas).

SPECIMENS. **Guatemala**: Quezaltenango, Volcán Santo Tomás, 2500–3700 m, 22.I.1940, *Steyermark* 34760 (F, holotype), 34774 (F). **Mexico**: Chiapas, Volcán Tacana West, 2800 m, 30.iii.1939, *Matuda* 2894 (F, MEXU, MICH, NY, US), S-228 (MICH).

(*b*) *Definition of the Hypericeae*

If one accepts the Englerian classification of the Hypericoideae as a subfamily of the Guttiferae, then the inclusion of *Santomasia* in the Hypericeae necessitates an enlargement of the circumscription of this tribe (cf. Robson, 1977 : Table 2). The characters of the three tribes of the subfamily as now constituted are shown in Table 2.

(*c*) *The affinities of the Hypericeae*

From Table 2 it is clear that the three tribes of the Hypericoideae are very different, so that there is no difficulty in assigning a given species to one of them. It is equally clear, when other subfamilies of the Guttiferae are considered, that none of them can have given rise to the Hypericoideae. The nearest one in many respects is the Kielmeyeroideae, which Maguire (1972) has (rightly in my opinion) united with the Bonnetiaceae. The family so formed has

Table 2 Characters of the tribes of the Hypericoideae

Tribe	Vismieae	Cratoxyleae	Hypericeae
Genera	*Vismia* Vand. *Psorospermum* Spach *Harungana* Lam.	*Eliea* Cambess. *Cratoxylum* Blume *Thornea* Breedlove & McClintock *Triadenum* Rafin.	*Santomasia* N. Robson *Hypericum* L.
Leaf venation	pinnate (co-arcuate)	pinnate (co-arcuate)	flabellate (pedati-flabellate) to pinnate (co-arcuate)
Inflorescence branching	thyrsoid, racemiform	thyrsoid, racemiform	dichasial or thyrsoid, dichasial
Sepals	5, quincuncial	5, quincuncial or irregularly imbricate	5, quincuncial or 4, decussate
Petals	5, white or greenish to yellow or orange, nearly always internally villous, without or rarely with ligule	5, white or greenish to pink or crimson, glabrous, without or with ligule	5–4, yellow to orange, often ± suffused with red, glabrous, without or very rarely with ligule
Fasciclodes	5	3 (4–5)	0 or very rarely 5 or 3
Stamen fascicles	5, free	5, united 2 + 2 + 1 (very rarely 2 + 1 + 1 + 1 or free)	5, free or united 2 + 2 + 1 (rarely 2 + 1 + 1 + 1) or 5–4 wholly united
Styles	5, free	3 (4–5), free	5–2, free or ± united
Placentation	5, axile	3 (4–5), axile	5–2, axile to parietal
Fruit	baccate (∞–5-seeded) or drupaceous (5 pyrenes)	capsular	capsular or rarely baccate or tricoccoid
Dehiscence	indehiscent	loculical or septicidal or both	septicidal or rarely indehiscent
Seed	not winged or carinate, sometimes gland-dotted	winged or not, not gland-dotted	winged or carinate or not, not gland-dotted
Cotyledons	equal, straight or unequal, curved to inrolled	equal, straight	equal, straight

Data from Engler (1925), Perrier de la Bâthie (1951), Ewan (1962), Bamps (1966), Gogelein (1967), Baas (1970), Robson (1974).

characters that bridge the gap between the Guttiferae and Hypericaceae of Bentham (1862) (who excluded the Kielmeyeroideae from both families), on the one hand, and the Theaceae sensu stricto (i.e. the subfamilies Camellioideae and Ternstroemioideae) on the other. For example, in it are included genera with latex (e.g. *Kielmeyera*, *Neotatea*) and without it (e.g. *Bonnetia*), with leaves alternate (e.g. *Archytaea*) or opposite (e.g. *Marila*)—even rarely stipulate (*Mahurea*), without oil-glands (e.g. *Archytaea*) or with them (e.g. *Caraipa*), and with petals that are imbricate (quincuncial) in bud (e.g. *Neogleasonia*) or contorted (*Kielmeyera*).

Although these intermediate characters would suggest that the Bonnetiaceae is primitive relative to the Guttiferae sensu lato, they are accompanied by more specialised characters which indicate that the relationship is not a simple one. Thus, the only genera in the Bonnetiaceae in which the antisepalous stamen whorl occurs are *Ploiarium* and *Archytaea* (Kobuski, 1950), where it is sterile and much reduced in size. These genera are also the only ones with a 5-merous gynoecium. On the other hand, their leaf-venation is, as we have seen, more advanced than the most primitive state in *Hypericum*. We can say, therefore, that the Bonnetiaceae and the Guttiferae arose from the same stock, but not that the former gave rise to the latter. Even if one goes further back along the evolutionary line of the Dilleniidae to the Dilleniaceae itself (*pace* Corner (1976), who denies that they are on the same line), it is not possible to find a direct ancestor of the Guttiferae. Although the Dilleniaceae includes species with floral characters that are more primitive than corresponding ones in the Guttiferae (e.g. the apocarpous ovary), yet there are other respects in which all its members are more advanced than the most primitive species of Guttiferae and Bonnetiaceae (e.g. the pinnate leaf-venation (Rury & Dickison (1977)). It would therefore seem, not surprisingly, that the ancestral species linking the Dilleniaceae, Bonnetiaceae and Guttiferae are extinct or still to be discovered.

To return to the Hypericoideae, whereas the most primitive leaves in *Vismia* (e.g. in *V. japurensis* Reichardt) resemble those of the Bonnetiaceous *Marila*, for example, and the stellate indumentum present in most of the Vismieae is comparable and possibly homologous with that in *Caraipa*, its floral characters are partly more primitive and partly more advanced—more primitive in the better-developed staminodial whorl, more advanced in having internally villous petals, stamen filaments in each fascicle united above the middle, and baccate fruit. The pinnate leaf-venation in the genera of the Cratoxyleae is likewise advanced relative to the most primitive state in the Bonnetiaceae ('parallel'); and the usual trimery in the inner floral whorls is another relatively advanced character, which is associated with erect petals and united filaments, as in the Vismieae. Yet, here again the staminodial whorl is better developed than in *Ploiarium* and *Archytaea*. The Hypericeae, on the other hand, are at the same evolutionary stage as the Bonnetiaceae as regards the development of the staminodial whorl, apart from the 'Elodes' group, in which, as has already been shown (Robson 1972*a*, 1977*a*), it appears to have been re-acquired. The presence of five fascicles of stamens is a primitive character within the Hypericeae (Robson, 1977*a*, see also below, p. 100), and such fascicles occur in the Bonnetiaceae only in *Ploiarium* and *Archytaea*, the androecium of the other genera being at the evolutionary level of, say, *Hypericum* sect. 20. *Myriandra*. But, even in these two genera, the filaments are united above the base. We can therefore conclude that no tribe of the Hypericoideae is wholly advanced in character with respect to the Bonnetiaceae, even though the latter is in general more primitive.

In a recent study of the wood anatomy of the Bonnetiaceae, Baretta-Kuipers (1976) upheld Maguire's view that it is a family quite distinct from the Theaceae. Excluding *Kielmeyera*, which is somewhat different from the others, she found that in wood structure the genera together form a gradual transition from Theaceae to Guttiferae. She also suggested that *Poeciloneuron* Beddome, a genus of two species from south-western India placed by Engler (1925) in the Guttiferae–Calophylloideae, might be incorporated into the Bonnetiaceae.

It seems clear, therefore, (i) that the relationships of the Hypericoidae to the Bonnetiaceae are just as close as they are to other subfamilies of the Guttiferae and (ii) that the circumscription of some of these subfamilies is still not wholly certain. In these circumstances I would suggest that the Bonnetiaceae be incorporated in the Guttiferae as a subfamily co-ordinate with the Hypericoideae, Calophylloideae, Moronobeoideae, Clusioideae and Garcinioideae (probably distinct from the Clusioideae), thus making the Guttiferae an entity which is natural and well separated from adjacent families.

Kubitzki (1978), in his study of *Caraipa* and *Mahurea*, comes to similar conclusions regarding the inclusion of the Bonnetiaceae in the Guttiferae and further points out that the former differ from the Theaceae sensu stricto in having rubiaceous stomata, in certain wood characters (cf. Metcalfe & Chalk, 1950) and in the occurrence of xanthones (Lima, Gottlieb & Lins Mesquita, 1972). The last character, in particular, is typical of the Guttiferae.

2. Methodology

Before we turn to detailed consideration of *Hypericum*, a short outline of the philosophical basis of the work and the consequent methods employed in it may be helpful.

Evolution and classification

In the absence of a useful fossil record—and, with the possible exception of Pliocene seeds (see e.g. Reid, 1923), there are no known fossils of *Hypericum*—evolutionary data must be obtained from recent forms. Self-evident and a truism though this statement may be, there is no general agreement yet about the validity of data obtained from this source. One still encounters the affirmation that all such data are merely speculative and thus 'unscientific.' On the other hand, the publication of numerous papers in which evolutionary aspects of contemporary organisms are discussed indicates that many biologists do not share this view. Much has also been written about the relation between evolution and classification, ranging from a denial that they are related ('phenetic' classifications) to the publication of 'evolutionary' or 'cladistic' classifications. Workers who take an intermediate position in this debate (e.g. Mayr, 1968) have suggested that a classification should reflect the evolutionary history of the group as closely as possible. There is no group of recent organisms of which all the members still exist, and so all classifications of such organisms involve hypotheses concerning the relationships within the group. Incidentally, the same can be said of classifications that do include fossils. It is the existence of gaps in the range of variation due to absent members of a taxonomic group that enables us to classify at all. Classification is thus an analytical process. In order that the analysis may result in taxa that are monophyletic and that together reflect the apparent course of evolution in the group, it is desirable first to perform a synthesis, i.e. to construct a phylogenetic scheme. 'First look for the similarities, then the differences.' By so doing, the chances of misclassification are minimised, and the resultant classification is more likely to be natural, i.e. to represent the actual variation pattern in hierarchical categories. Subsequently the gaps in variation, and hence the limits of the taxa, can be determined.

From the above considerations it will be seen that the problem in *Hypericum* classification, as it would be in that of all wholly recent taxa, has been to obtain evolutionary data and construct a phylogenetic scheme using non-fossil data only.

Trends and taxonomy

One of the most serious criticisms that are levelled at herbarium taxonomy is that it is concerned mainly with adult structures, whereas evolution involves repeated ontogenies. Although the use of more-widely-based evidence goes some way towards answering this criticism, it is still true that classical taxonomy tends to be static in concept, whilst evolution is a dynamic process. For this reason I have reservations about the usefulness of neo-Adansonian methods of classification—and indeed about all methods involving maximum correlation of individual characters. Being based on the static 'character' concept, they cannot be relied upon to produce a natural classification (cf. Mayr, 1968). On the other hand, the dynamic aspect of evolution is reflected in character trends, i.e. directional changes in a character through time. Any taxon has both stable and variable characters; and whereas character-correlation methods tend to treat only the stable ones satisfactorily, the variable characters are those that produce the trends and can therefore be important indicators of affinity.

Trends can be observed equally well in fossil and recent material; and there seems to be no good reason why spatial trends (i.e. those observable in geographically displaced taxa) should be regarded as less 'valid' than those derived from a chronological sequence of fossils. The difference between the two types is merely that the trends are manifest in a reasonably complete fossil sequence, whereas they have to be worked out for contemporaneous taxa. Of course, 'working out' is also necessary for all but the most complete series of fossils, so that the need for hypotheses is rarely less for them than it is for recent organisms. If the validity of interpreting character trends among contemporaneous taxa as evolutionary trends is admitted, there still remain the problems of recognising them and interpreting their direction correctly. These topics have recently been discussed in detail by Stebbins (1974; ch. 70), who pointed out that, although trends in single characters are sometimes reversed, if trends are based on simple alterations of the development pattern, the more complex and multifactorial the basis of a character is, the less reversible it will be. It follows that, if one correlates *trends* rather than characters, then chances of being misled by convergence or parallelism are minimised and general evolutionary directions can be accurately established. It is usually more difficult to establish the true direction of a trend than to recognise the trend itself. Hennig (1966*a*) and Stebbins (1974) both discuss the criteria by which trend direction may be discovered; but during the present work the direction of a given trend had often had to be assumed initially. Subsequent correlation with other trends and distributional data has almost always indicated whether or not the original assumption was valid. By this method it has usually been possible to build up a coherent broad evolutionary picture, with a fair degree of confidence in its accuracy.

Constructing phylogenetic diagrams

The size of *Hypericum* (over 400 species) would preclude the extensive use of numerical methods of character assessment, even if it had been thought desirable to use them, and so the process of recognising and correlating trends has been largely one of inspection. If a search is made for the 'nearest neighbour' of each species, then an affinity diagram such as is shown in Fig. 5 (p. 70) will result. This diagram differs from a Hennigian sister-group one in showing some multiple affinities because it is based on overall resemblance. Hennig is no doubt correct in assuming that, for practical purposes, each monophyletic taxon originates at one time from one ancestral taxon, so that only two sister-groups are thereby formed. Nevertheless, variation in (say) a species may occur in several morphological and geographical directions at once. If it is split into more than two parts and speciation subsequently occurs, each sibling species will include a different part of the variation of the original species. The actual order in which the parts are split off may be evolutionarily interesting; but to make it the basis of classification, as adherents of the Hennigian school advocate, seems to be unnecessary.

The published sectional classification diagram of *Hypericum* (Robson, 1977*a*: figs 1, 2), which is reproduced in a slightly improved form in Fig. 2, shows examples of sections with multiple derivatives and more than one hidden example of paraphyly (i.e. of a taxon that does not include all the derivatives of its ancestral group). One paraphyletic line comprises sects 27. *Adenosepalum* and 28. *Elodes*, as the latter (monotypic) section is apparently related to relatively advanced members of the former. Nevertheless, the transition from open pollination to specialised pollination, with accompanying profound morphological modifications (Robson, 1977*a*: 298–302), provides a conspicuous gap in variation which, I think, should be reflected in the classification. Admittedly the rank to adopt is a matter of judgement, but so it is in many taxonomic decisions. With regard to the sections with multiple derivatives, the detailed relationships of each one can be represented in a cladistic diagram such as Fig. 3. The broken line defining sect. 1. *Campylosporus* includes all those species with regularly pentamerous flowers, persistent petals and stamen fascicles, and at least partly united styles. All gaps in variation to the outside of this line are considerable and easily recognised, with the exception of that separating sect. 1. *Campylosporus* from sect. 3. *Ascyreia*. Here two of the key characters (i) persistent versus deciduous petals and stamens and (ii) united versus free styles are not completely reliable in *H. socotranum*. Nevertheless,

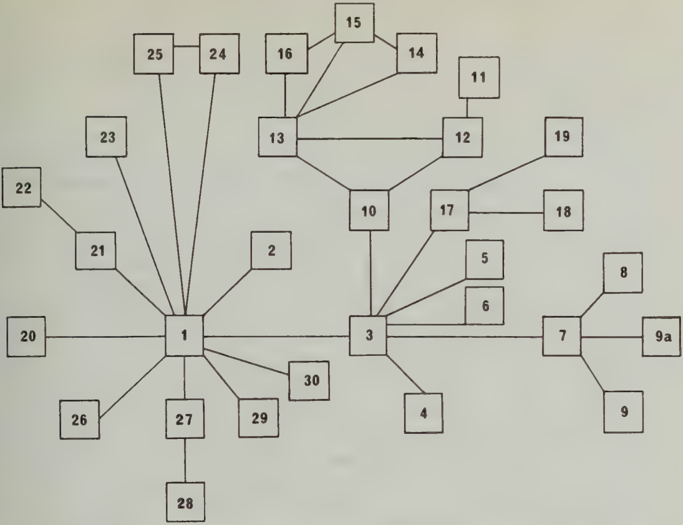


Fig. 2 Affinities of sections of *Hypericum*, slightly modified from Robson (1977*a* : figs 1, 2).

the complete geographical segration of the two taxa and the fact that united styles recur only in advanced species of sect. *Ascyreia* (e.g. *H. monogynum*) allow one to recognise them as sections. The forked line to sects 24 and 25 indicates that the relative advancement of these sections is not clear. Thus, although the vegetative parts in sect. 24. *Heterophylla* (*H. heterophyllum*) are more advanced (e.g. in having the leaf-differentiation from which it gets its name) and its distribution suggests a derived relative position, the flowers are homostylous, whereas in sect. 25. *Adenotrias* they are heterostylous. The evolutionary diagrams of sections (e.g. Fig. 5) have been produced by stages, in a way rather similar to building up a jigsaw-puzzle picture. Certain primitive/advanced relationships are usually obvious; but, even if the trend directions in them are not clear at first, small separate 'pieces' of the diagram can be constructed on the basis of overall similarity. In theory, the whole diagram could be produced in this way (Fig. 4); but in practice it and others like it have resulted from a consideration of trends at an early stage. Thus its conversion into an evolutionary hypothesis by the insertion of (i) directional indications and (ii) the 'nearest neighbour' or 'sister group' to the whole section (Fig. 5) was not an entirely separate process. The two stages, however, show some similarity to the ground plan/divergence diagrams produced by Wagner (1952*a*, *b*) and subsequently elaborated by him and others (e.g. Wagner, 1969; Farris, 1970). The first-stage (interrelationship) diagram corresponds to the 'Wagner network' and the second (cladal) to the 'Wagner tree' (Nelson & Van Horn, 1976), but a numerical basis is lacking (for the reason stated above); and in my opinion it is unnecessary. Although in the early stages the diagram usually consists of separate linear series of taxa, based on trends in few characters, as other trends are gradually correlated, these linear series become 'fixed' in the picture. One therefore has a reasonable amount of confidence that the final diagram does show actual relationships, at least in broad outline; and it is possible to test its accuracy to some extent.

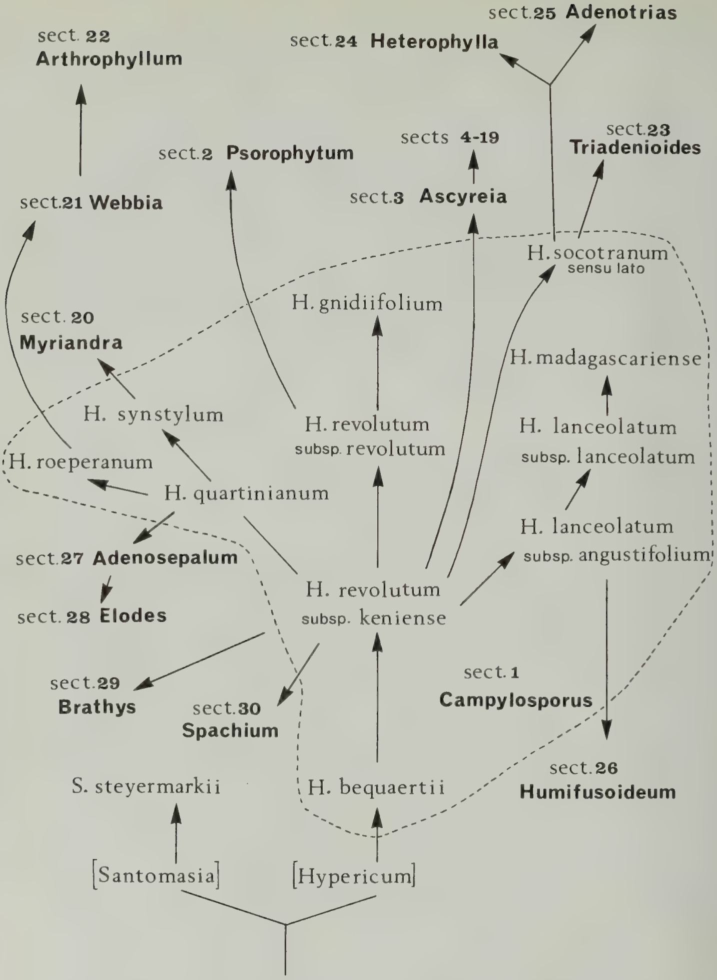

sect.25 **Adenotrias**
sect.24 **Heterophylla**
sect. 22 **Arthrophyllum**
sects 4-19
sect.23 **Triadenioides**
sect.2 **Psorophytum**
sect.3 **Ascyreia**
sect.21 **Webbia**
H. socotranum sensu lato
H. gnidiifolium
sect. 20 **Myriandra**
H. madagascariense
H. synstylum
H. revolutum subsp. revolutum
H. lanceolatum subsp. lanceolatum
H. roeperanum
H. quartinianum
H. lanceolatum subsp. angustifolium
sect.27 **Adenosepalum**
H. revolutum subsp. keniense
sect. 28 **Elodes**
sect. 1 **Campylosporus**
sect.29 **Brathys**
sect.30 **Spachium**
sect.26 **Humifusoideum**
S. steyermarkii
H. bequaertii
[Santomasia]
[Hypericum]

Fig. 3 Sect. 1. *Campylosporus*, showing its limits (dotted line) and the interrelationships within and outwith the section. For revised position of *H. gnidiifolium*, see footnote on p. 187.

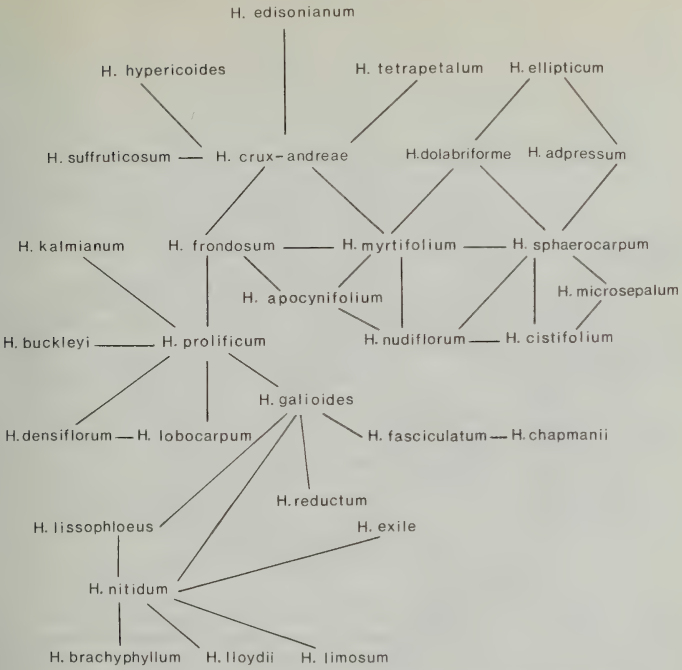

H. edisonianum
H. hypericoides
H. tetrapetalum
H. ellipticum
H. suffruticosum
H. crux-andreae
H.dolabriforme
H. adpressum
H. kalmianum
H. frondosum
H. myrtifolium
H. sphaerocarpum
H. apocynifolium
H. microsepalum
H. buckleyi
H. prolificum
H. nudiflorum
H. cistifolium
H. galioides
H.densiflorum
H. lobocarpum
H. fasciculatum
H.chapmanii
H.reductum
H. lissophloeus
H. exile
H. nitidum
H. brachyphyllum
H. lloydii
H. limosum

Fig. 4 Relationships in sect. 20. *Myriandra*, based on overall similarity (Stage I).

Testing the diagram

The earlier efforts to produce a classification of *Hypericum* (Choisy, 1821, 1824; Spach, 1836*a*, *b*, *c*; Keller, 1893, 1925) resulted in schemes that were partly gradal, i.e. based on corresponding stages of evolutionary development, not on descent; and the general aim of the present studies has been to convert these gradal schemes into a cladal one. The lines on the evolutionary diagrams, therefore, all indicate trends, and it should be possible to indicate the points of corresponding character-change (i.e. gradal points) along each line. Joining these points should produce concentric 'contour' curves or circles, depending on whether the primitive taxon is on the margin of the diagram or not (Robson, 1977*a*: Fig. 1). If, however, (a) the character change has taken place independently more than once (i.e. if the advanced character is polyphyletic), or (b) trend-reversals have occurred or (c) a trend has been misinterpreted, then two or more non-concentric circles will result. Thus Fig. 6 shows that in *Hypericum* there has been a trend from five styles to three or sometimes two; but in four sections (13, 15, 26, 30) there has been a reversion to five styles. Of course, as with hypotheses in general, the diagram can also be checked by adding data not used in its construction.

In conclusion, it should be stated that, although the above method of constructing and testing evolutionary diagrams was developed independently, no part of it is wholly original.

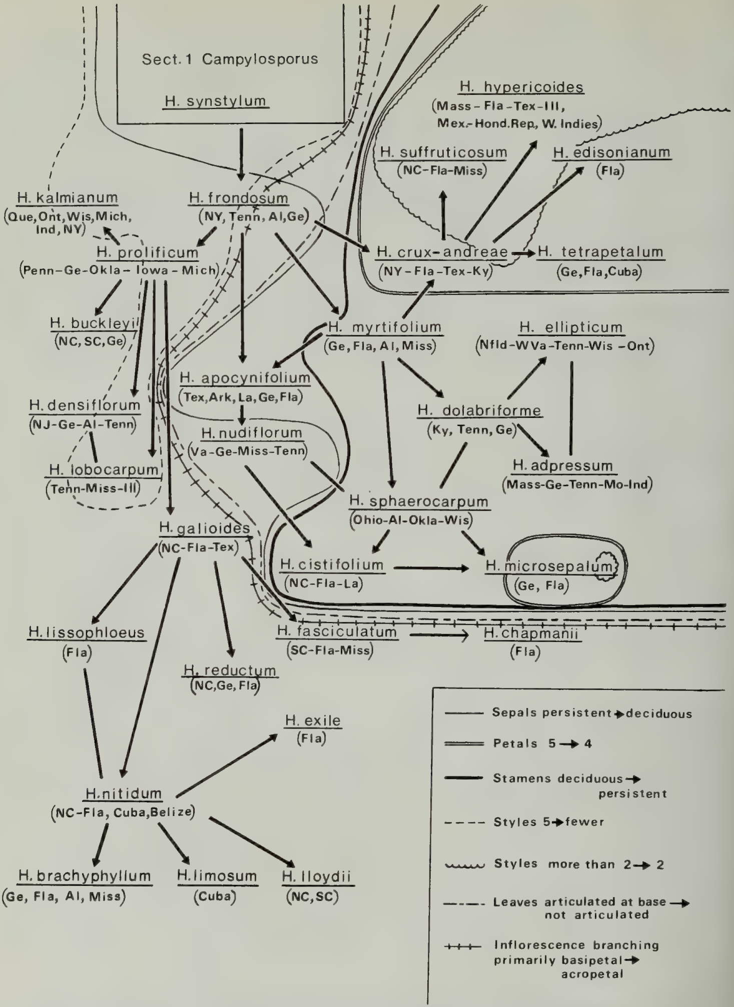

Sect. 1 Campylosporus
H. synstylum
H. hypericoides
(Mass - Fla - Tex - Ill,
Mex.-Hond.Rep., W. Indies)
H. suffruticosum
(NC-Fla-Miss)
H. edisonianum
(Fla)
H. kalmianum
(Que, Ont, Wis, Mich,
Ind, NY)
H. frondosum
(NY, Tenn, Al, Ge)
H. prolificum
(Penn-Ge-Okla - Iowa - Mich)
H. crux-andreae
(NY - Fla - Tex - Ky)
H. tetrapetalum
(Ge, Fla, Cuba)
H. buckleyi
(NC, SC, Ge)
H. myrtifolium
(Ge, Fla, Al, Miss)
H. ellipticum
(Nfld - WVa - Tenn - Wis - Ont)
H. apocynifolium
(Tex, Ark, La, Ge, Fla)
H. densiflorum
(NJ-Ge-Al-Tenn)
H. dolabriforme
(Ky, Tenn, Ge)
H. nudiflorum
(Va-Ge-Miss-Tenn)
H. adpressum
(Mass-Ge-Tenn-Mo-Ind)
H. lobocarpum
(Tenn-Miss-Ill)
H. sphaerocarpum
(Ohio-Al-Okla-Wis)
H. galioides
(NC-Fla-Tex)
H. cistifolium
(NC-Fla-La)
H. microsepalum
(Ge, Fla)
H. lissophloeus
(Fla)
H. fasciculatum
(SC-Fla-Miss)
H. chapmanii
(Fla)
H. reductum
(NC, Ge, Fla)
H. exile
(Fla)
H. nitidum
(NC-Fla, Cuba, Belize)
H. brachyphyllum
(Ge, Fla, Al, Miss)
H. limosum
(Cuba)
H. lloydii
(NC, SC)
Sepals persistent → deciduous
Petals 5 → 4
Stamens deciduous → persistent
Styles 5 → fewer
Styles more than 2 → 2
Leaves articulated at base → not articulated
Inflorescence branching primarily basipetal → acropetal

Fig. 5 Relationships in sect. 20. *Myriandra*, showing evolutionary trends and also some character limits (Stage II).

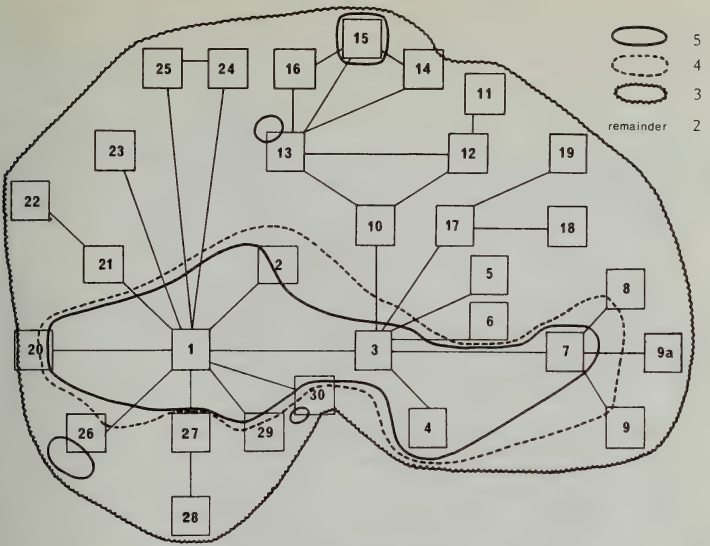


Fig. 6 Variation in style number in *Hypericum.*

Thus, the resemblance of the diagrams to Wagner trees has already been pointed out; and character-limits have been shown on evolutionary diagrams by several authors (e.g. Kubitzki, 1969; Dahlgren, 1977). Nevertheless, the method has proved to be useful in studying the cladistic relationships of a large number of species without resorting to time-consuming numerical methods; and from the resultant diagrams it is usually relatively easy to decide how to classify and key out the group.

Geographical aspects of evolutionary diagrams

Because evolution usually takes place in space as well as time, there is a distributional component to most evolutionary trends. It is therefore possible to retrace on a map changes that have taken place over a period of time. This is one way of checking an evolutionary hypothesis—it must make geographical sense. Thus, in an evolutionary line one is likely to find that the most primitive taxon has a restricted distribution, the early derivatives are more widespread and frequently occur in disjunct areas, and the most recently evolved taxa either are the most widespread or show signs of having evolved from a widespread taxon (neo-endemics). A trend in sect. 26. *Humifusoideum* (*H. natalense* → *H. wilmsii* → *H. peplidifolium*) provides a good example (Fig. 7).

Hennig (1966*a*, *b*) proposed three Biogeographical Rules, which have been formalised and extended by Ashlock (1974). These are intended to summarise the relationships between phylogeny and geography. The trend shown in Fig. 7 is an illustration of the Progression Rule: The direction of progression of a geographical sequence of taxa is indicated by a series of increasingly derived synapomorphic characters. If a group of organisms fits this rule, then it is an indication that its history has not been seriously disturbed e.g. by extensive hybridisation. The other two Hennigian rules, the Phylogenetic Intermediate and the

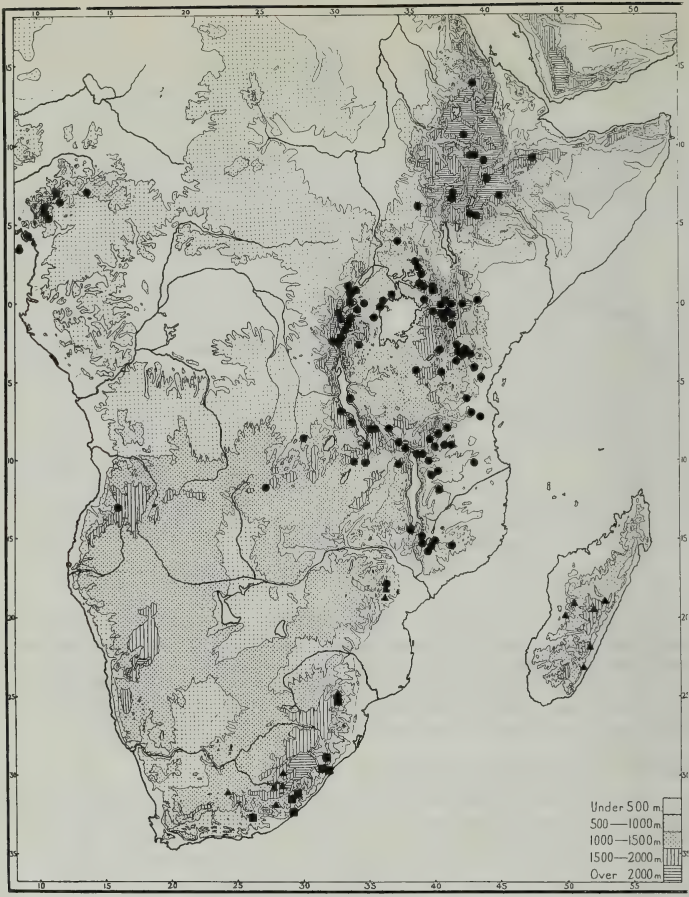

Under 500 m.
500—1000 m.
1000—1500 m
1500—2000 m.
Over 2000 m
10
15
20
25
30
35
40
45
50
55

Fig. 7 Distributions of African members of sect. 26. *Humifusoideum*. ■ *H. natalense*, ▲ *H. wilmsii*, ● *H. peplidifolium*.

Multiple Sister-Group Rules, which refer to relationships between taxa on different continents, and Ashlock's (1974) fourth rule, the Drift Sequence Rule, which relates these to the theory of Continental Drift, concern topics that will be considered later (Chapter 10).

In addition to these Biogeographic Rules, the following three more or less self-evident points have been borne in mind:

(i) The more primitive the taxon, the more likely it is to have had a past distribution markedly different from its present one in location and/or extent.

(ii) Anomalies in distribution (such as wide disjuncts) that cannot be due to climatic or intracontinental physiographic change alone should be interpreted in terms of either Continental Drift or long-distance dispersal; but Occam's Razor should discourage the invocation of a long-distance dispersal hypothesis until or unless theories based on normal dispersal distances prove to be untenable.

(iii) Long-distance-dispersal theories, when they have been proposed, should be related to methods of dispersal.

Using the above criteria, the only section in which evidence of long-distance dispersal has been found in *Hypericum* is sect. 30. *Spachium*, where it appears to have occurred in several groups among the most specialised members, all of which grow in damp habitats.

3. Morphology

Habit

Species of *Hypericum* exhibit a wide range of habit forms from the arboreal to the ephemeral. At one extreme, some species in sect. 1. *Campylosporus* (e.g. *H. bequaertii*) can form trees up to12 m high, with a true single trunk; at other extremes one finds, for example, *H. gentianoides* (sect. 30. *Spachium*), an annual herb with leaves reduced to scales, and *H. elodes* (sect. 28. *Elodes*), which can produce threadlike stems in water up to 50 cm deep (Glück, 1911).

True trees, however, are rare and occur only among the most primitive species of the most primitive sections (1. *Campylosporus*, 3. *Ascyreia*, 29. *Brathys*). Most of the woody species are many-stemmed, with the main branches erect or suberect. The laterals may spread to some extent; but only in relatively advanced species does one find all the branches spreading with co-planar leaves. This effect can be so pronounced as to give a frondose appearance to the whole shoot (e.g. in *H. uralum*, sect. 3. *Ascyreia*). The lowermost branches in these shrubs may arise from below soil level, but they do not normally root, even in the dwarf shrubs such as *H. olympicum* (sect. 10. *Olympia*) which are on the border of woodiness.

Among perennial herbs, however, the situation is different. Many of these spread at or near ground level by means of runners, which grow horizontally for some distance before becoming erect or ascending, and the horizontal nodes frequently produce roots. In *H. elodes* this habit has become very well developed, as it has in some other species of wet habitats (e.g. *H. scioanum*, sect. 30. *Spachium*). In other species a true rhizome is found (e.g. in *H. adpressum*, sect. 20. *Myriandra*). At least two species also produce vegetative buds from the roots, *H. perforatum* (sect. 9. *Hypericum*) and *H. pulchrum* (sect. 18. *Taeniocarpium*), a phenomenon which may partly explain the abundance of these species in western Europe (Salisbury, 1942). The successful establishment of *H. perforatum* after introduction into other parts of the world, however, is more likely to relate to its methods of seed production.

The annual species, which of course all have perennial ancestors, do not show this propensity for rooting at the nodes. The transition may be observed in *H. humifusum* (sect. 14. *Oligostema*), for example, in which the perennial forms tend to have rooting shoots whereas the annual ones ('*H. liottardii* Vill.') have only the tap-root system.

Stems

(*a*) *Stem-lines and phyllotaxis*

The co-ordination of leaf-initiation in *Hypericum* is always complete, so that the phyllotaxis is always either opposite-decussate or rarely 3–4-whorled. In this respect it resembles all the other genera of the Guttiferae except most members of the Bonnetioideae and some species of *Psorospermum* Spach. In this genus the phyllotactic co-ordination breaks down in the upper parts of the stem of some species (e.g. *P. alternifolium* J. D. Hook.), resulting in secondarily alternate leaves.

Associated with the opposite-decussate phyllotaxis is the occurrence of four raised lines on the younger parts of the stem in many species (Fig. 8a). This appears to be the primitive

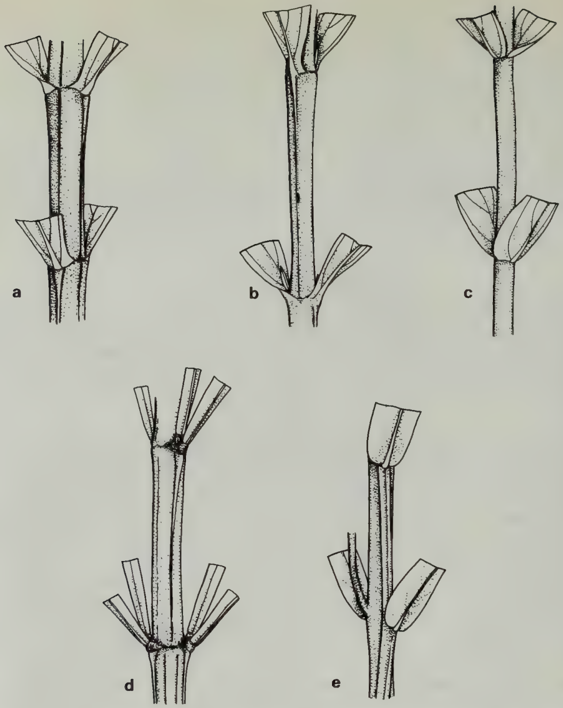


Fig. 8 Stem lines in *Hypericum* and *Ploiarium*: (a) *Hypericum revolutum*; (b) *H. perforatum*; (c) *H. bithynicum*; (d) *H. nitidum*; (e) *Ploiarium alternifolium*.

state in *Hypericum*; and it gives rise to 2-lined and then terete conditions, either by development (on the same woody shoot) or evolution (in some herbaceous species) (Fig. 8b, c). Occasionally six lines may be present in some internodes, e.g. in some species of sect. 20. *Myriandra* (Fig. 8d). Although these structures are usually no more than 'raised lines', they can be wide enough to be termed 'wings' (e.g. in *H. tetrapterum*, sect. 9. *Hypericum*). The members of an opposite pair are always equally prominent; but there is almost always some difference between alternating pairs so that the lines decurrent from the leaf-bases (medians) are more prominent than those from between the leaves (laterals). Consequently, where there is only one pair of lines, these will almost always be medians. The exceptions to this rule occur in sect. 5. *Androsaemum*, where the sometimes 4-lined *H. hircinum* has laterals that are more prominent than the medians and the 2-lined *H. androsaemum* has laterals only.

The association of stem-lines with leaves is clearer in *Ploiarium alternifolium* (Bonnetioideae), in which the presence of stem-lines in the youngest parts is combined with spiral phyllotaxis. Although the lines are sometimes faint, three can be seen below each leaf, decurrent respectively from the midrib and each side of the petiole (Fig. 8e). It would appear, then, (i) that the stem-lines are related morphologically to the leaves, (ii) that the opposite-decussate phyllotaxis in *Hypericum* usually results in the lateral lines uniting in pairs (4-lined stems), but that (iii) they occasionally remain distinct (6-lined stems). In the occasional species or forms with 3–4-whorled leaves (e.g. *H. empetrifolium*, sect. 19. *Coridium*; *H. ternatum*, sect. 23. *Triadenioides*; *H. ternum*, sect. 30. *Spachium*), the number of lines equals the number of leaves, i.e. only medians are present.

Evidence produced by Noack (1939) from crosses between *H. perforatum* L. (2-lined, tetraploid) and *H. maculatum* subsp. *maculatum* (4-lined, diploid) (sect. 9. *Hypericum*) indicates that the presence of lateral lines in this group is an incompletely dominant character, the triploid hybrids (*H.* x *desetangsii* Lamotte nm. *carinthiacum* (Fröhl.) N. Robson) having very narrow or incomplete laterals.

(*b*) *Woody stems*

In the shrubby and arborescent species the internodes eventually become terete, although the lines may remain in evidence for a considerable time (e.g. in *Hypericum revolutum*, sect. 1. *Campylosporus*). The young stems may be green or vinous red, but the secondary ones are smooth (sometimes even 'polished') and reddish or brownish-red to cinnamon at first, without any visible lenticels. They may eventually become almost black. In most species vertical fissures then appear and the cork layers turn pale grey and flake off in strips. Sometimes, however, for example in *H. frondosum* and *H. lissophloeus* (sect. 20. *Myriandra*), these vertical fissures do not appear and the cork layers exfoliate in larger patches, as in species of *Betula*.

In *H. chapmanii* (also sect. *Myriandra*), Adams (1962*a*) describes a soft spongy bark up to 4 cm thick, of which the outer layers disintegrate and fall away, leaving more-resistant strips of hardened laticifers. Other species in this section (e.g. *H. tetrapetalum*) have less spongy bark, and in other sections it rarely becomes markedly corky.

The stems can eventually attain a diameter of 15 cm (in *H. chapmanii*) or more (in some species of sects 1. *Campylosporus* and 29. *Brathys*).

(*c*) *Stem glands*

The epidermis of herbaceous stems in *Hypericum* sometimes contains small, round or somewhat elongated glands similar to those occurring in the leaves (cf. pp. 80–82). These may be colourless, reddish or black, depending on the concentration of hypericin present in them, and they may be confined to the stem lines (sect. 9. *Hypericum*) or dispersed over the whole stem (sects 12. *Origanifolia*, 17. *Hirtella*). In sect. *Hirtella* the glands vary in colour and prominence. Thus, in *H. lydium* they range from colourless to reddish, and the reddish ones may be distinctly prominent ('*H. adenocladum*' Boiss.). This last trend is more marked in the typical variety of *H. scabrum*, in which the reddish stem glands are on short unbranched protuberances, giving the stem the roughness that suggested the epithet 'scabrum'; and in *H. thymopsis,* which is derived from *H. scabrum*, the gland-tipped protuberances toward the base of the stem are branched.

Vestiture

Apart from glandular emergences, the only vestiture that occurs in *Hypericum* consists of simple uniseriate hairs. No stellate hairs, such as those that are a feature of the Vismieae, are found. Members of the primitive sections are wholly glabrous or have a minutely papillose leaf epidermis (e.g. *H. revolutum* subsp. *keniense* (Schweinf.) N. Robson, sect. 1. *Campylosporus*) (cf. Spirlet, 1967), but an indumentum has developed independently in several advanced groups of species. Thus, species in sects 1–10 and 13–16 are wholly glabrous, except for the Bulgarian *H. setiferum* (sect. 13. *Drosocarpium*), which differs from *H. montbretii* only in having sparse appressed hairs on the lower surface of the leaf and is probably not specifically distinct from it. The stem, leaves and sepals of various species in sects 11. *Campylopus*, 12. *Origanifolia*, 17. *Hirtella* and 18. *Taeniocarpium* are scabrid-papillose to hirsute, but the hairs remain distinct and spreading. Likewise, in the only species in sect. 30. *Spachium* with indumentum (*H. setosum*), the hairs are distinct and relatively short.

All the remaining hirsute species are found in sect. 27. *Adenosepalum* and its 'satellite' sect. 28. *Elodes*, and among them only in species of northern Africa, Macaronesia, Europe and western Asia. In *H. reflexum*, from Macaronesia, only the stem is pubescent, and the European and N. African *H. montanum* is wholly glabrous or has a scabrid lower surface of the leaf. Otherwise, where hairs are present they are distributed over the stem, leaves and sepals (outer surface only), and they sometimes become long and interwoven (e.g. in *H. tomentosum* and *H. elodes*).

Leaves

(*a*) *Insertion and margin*

Like most genera of the Bonnetioideae, the primitive species of *Hypericum* have sessile leaves. Where a petiole has evolved, it is never completely differentiated from the lamina, the transition being always gradual. Leaves with a relatively long petiole of this type occur in sects 9. *Hypericum* (e.g. in *H. petiolulatum*) and 27. *Adenosepalum* (e.g. in a form of *H. himalaicum* N. Robson), but species in several sections can be described as sub-petiolate. At the other extreme, six distinct species or species-groups with perfoliate leaves have evolved, viz. *H. bupleuroides* (sect. 8. *Bupleuroides*), *H. sampsonii* (sect. 9. *Hypericum*), *H. spectabile* (sect. 17. *Hirtella*), *H. pamphylicum* (sect. 22. *Arthrophyllum*—cf. Robson & Davis, 1980), *H. caprifolium* and *H. coadunatum* (sect. 27. *Adenosepalum*) and *H. connatum* and *H. caprifoliatum* (sect. 30. *Spachium*).

Associated with changes from shrubby to herbaceous habit there is a tendency towards retention of the leaves on the stem. Primitive species, therefore, have an articulation at the base of the leaf, whereas in advanced species this has disappeared (cf. Adams, 1962*a*).

The most primitive species in sects 1. *Campylosporus* and 29. *Brathys* have the leaf-base reflexed, suggesting an auricle, and the same structure occurs in *Santomasia steyermarkii*. In more advanced species of *Hypericum*, however, this structure has been lost; but true auricles have evolved in three sections, in each of which they are associated with gland-fringed leaf margins, thus providing the only exceptions to the rule that the leaves in the Guttiferae (excluding some Bonnetioideae) are entire. In two sections (viz. 15. *Thasia* and 16. *Crossophyllum*, i.e. in *H. thasium*, *H. orientale* and *H. adenotrichum*), the evolution of gland-fringed leaves and auricles seems to have been basipetal from the bracts, as auricles are less conspicuous in or absent from the lower leaves. In *H. vesiculosum* (sect. 13. *Drosocarpium*), on the other hand, it is the lower leaves that are gland-fringed, whereas the upper ones are entire and there is an abrupt transition to the narrow gland-fringed bracts (see also *Bracts and bracteoles*, p. 85).

(*b*) *Venation*

All species of *Hypericum* have a complete midrib, and the most primitive ones (*H. bequaertii*, *H. revolutum* subsp. *keniense* and *H. lanceolatum* subsp. *angustifolium* (Lam.) N. Robson—sect. 1. *Campylosporus* and *H. styphelioides*—sect. 29. *Brathys*) have 'parallel' venation. In order to understand the evolution of leaf venation within the genus, however, it is necessary to consider in more detail some members of allied genera that were discussed briefly in relation to *Santomasia* (p. 61).

In the Bonnetioid *Neblinaria celiae* Maguire (1972 : 155, f. 24) (Fig. 9a), the crowded leaves have a flat pseudopetiole which is entered by about seven leaf traces. These dichotomise considerably in the broad base of the leaf before radiating without further major branching to near the apex. The main veins are equally thick apart from the median one, which is somewhat thicker than the rest at the base and forms an embryonic midrib. In other leaves (e.g. that shown in Fig. 9a), there is a tendency for the veins adjacent to this midrib to

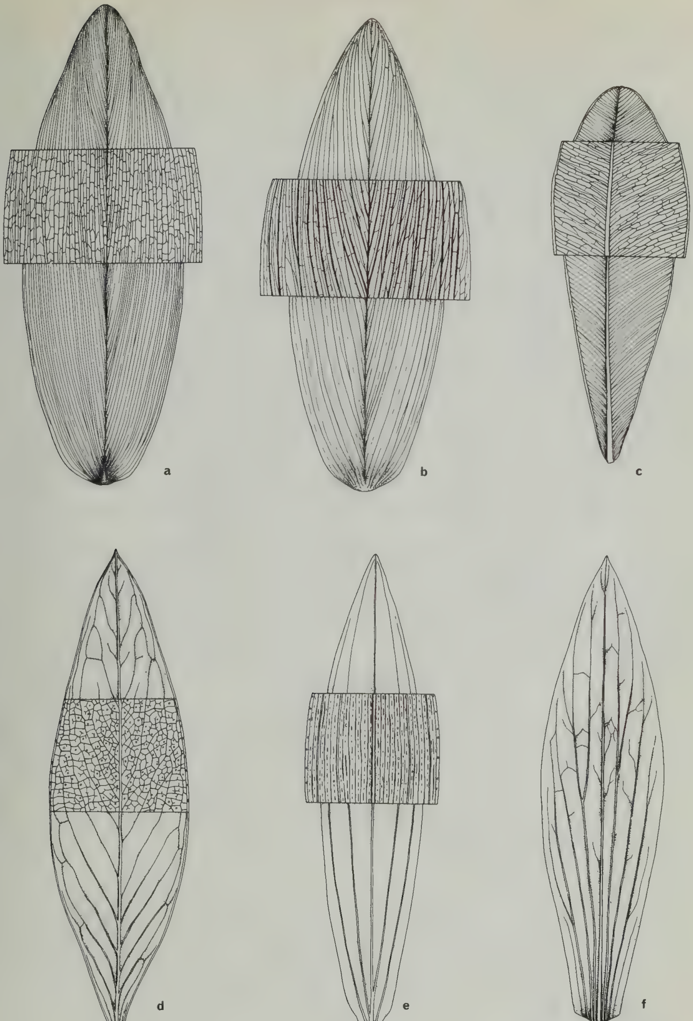
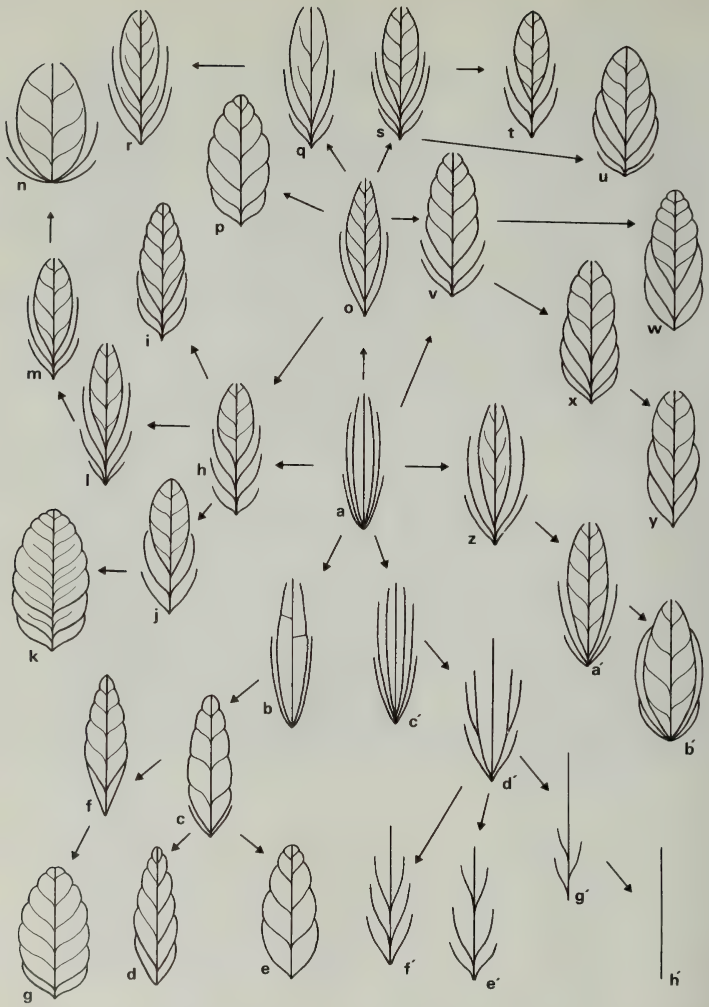


Fig. 9 Leaf-venation in some Bonnetioideae and Hypericeae, showing evolutionary trends: (a) *Neblinaria celiae* (x 1); (b) *Neogleasonia wurdackii* (x 1); (c) *Neotatea colombiana* (x 1); (d) *Santomasia steyermarkii* (x 2); (e) *Hypericum bequaertii* (x 2); (f) *Hypericum styphelioides* (x 5).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unite with it. Near the apex the main veins may dichotomise and anastomose to form a reticulum, but the margin itself is unveined. As we have seen above (p. 61), this venation is basically pedati-flabellate or parallelodromous, but the marginal anastomoses towards the apex show a tendency towards the development of an intramarginal vein.

Neogleasonia wurdackii Maguire (1972 : 160, f. 25), (Fig. 9b), also Bonnetioid, has less crowded leaves which do not narrow at the base. The leaf scars show one large central trace (which becomes a complete midrib) and four small lateral ones. Some or all these appear to dichotomise in the leaf base, as in *Neblinaria*; but the tendency for the veins nearest the midrib to become united with it is more marked, so that, in effect, the midrib is pinnately branched in the lower third or more. Another development from *Neblinaria* is that the veins have differentiated in 'size' so that thick ones alternate with thin ones. *Neogleasonia*, however, does not have marginal reticulation like *Neblinaria*.

In the third of Maguire's new Bonnetioid genera, *Neotatea* (Fig. 9c), the lateral veins are all decurrent into the midrib and the submarginal anastomoses have been consolidated, resulting in a densely pinnate venation (paxillate—Melville, 1976) with an intramarginal vein.

In *Santomasia* (Fig. 9d) the first of these trends is more advanced than in *Neogleasonia,* in that the process of union with the midrib has continued further. There are 6–10 lateral veins, of which the lower 4–5 are decurrent into the midrib and the rest (which are less distinct from the tertiary venation) join it at a definite, wider angle. As regards the number of its lateral veins, *S. steyermarkii* is more primitive than *Hypericum bequaertii* (Fig. 9e); but in-so-far as these are decurrent into the midrib, and in its densely reticulate tertiary venation and its glandularity (see p. 61), it is far more advanced. If one takes the numerous veins and incomplete midrib of *Neblinaria* as the primitive state, then *S. steyermarkii* is more advanced in having (a) fewer veins, (b) a complete midrib and (c) the veins united with the midrib.

The leaf-trace in *Hypericum* and *Santomasia* is unilacunar, as it is in all the Guttiferae so far investigated (including the Bonnetioideae) (Schofield, 1968). Maguire (1972 : 134) stated that the nodal anatomy of the Bonnetioid genera might not be consistent; but it seems reasonable to assume that they, too, are unilacunar, even though *Neogleasonia* and *Neotatea* have 3-trace leaf-scars (in *Neblinaria* they are 1-trace). If one accepts the hypothesis that the paired unilacunar trace is primitive in the angiosperms (cf. Schofield, 1968), then the incomplete midrib in *Neblinaria* can be conceived as derived by the partial union of the innermost branch of each trace.

Hypericum bequaertii is advanced relative to *Santomasia* in the trend towards a reduction in the number of veins. Thus, in *H. bequaertii* (Fig. 9e) there are only 3–5 major veins. On the other hand, these veins sometimes arise from dichotomies in the leaf-base (i.e. they are not always united with the midrib); and the leaf is at the *Neogleasonia* stage in having 5–7 thinner 'veins' alternating with the major ones.

Although these weaker 'veins' are apparently part of the same branching structure as the midrib and major basal veins, their connections with it are often absent. Thus one can sometimes follow such veins back through several dichotomies to the base of the leaf but find no

Fig. 10 Trends in major leaf-venation in *Hypericum* (numbers indicate sections): (a) *H. bequaertii* (1); (b) *H. revolutum* subsp. *keniense* (also *H. lanceolatum* subsp. *angustifolium*) (1); (c) *H. revolutum* subsp. *revolutum* (also *H. lanceolatum* subsp. *lanceolatum*) (1); (d) *H. madagascariense* (1); (e) *H. balearicum* (2); (f) *H. canariense* (21); (g) *H. cardiophyllum* (22); (h) *H. quartinianum* (1); (i) *H. roeperanum* (1); (j) *H. synstylum* (1); (k) *H. frondosum* (20); (l) *H. glandulosum* (27); (m) *H. lanuginosum* (27); (n) *H. elodes* (28); (o) *H. socotranum* (1); (p) *H. scopulorum* (23); (q) *H. lysimachioides* (17); (r) *H. hirsutum* (18); (s) *H. olympicum* (10); (t) *H. orientale* (16); (u) *H. bithynicum* (13); (v) *H. choisianum* (3); (w) *H. androsaemum* (5); (x) *H. elatoides* (7); (y) *H. pseudopetiolatum* (9); (z) *H. brasiliense* (30); (á) *H. silenoides* (30); (b́) *H. mutilum* (30); (ć) *H. styphelioides* (29); (d́) *H. magniflorum* (29); (é) *H. phellos* (29); (f́) *H. stenopetalum* (29); (ǵ) *H. struthiolifolium* (29); (h́) *H. brathys* (29). N.B. For amended position of f, g (sects 21, 22), see footnote on p. 187 and Fig. 3, p. 68.

clear connection with the main venous system. Indeed, they are not always continuous and have apparently lost (or are losing) their conductive function to become secretory structures. The conductive system has therefore been reduced to the midrib and two or four main basal or near-basal veins, none of which are branched. In other primitive species, e.g. *H. quartinianum* (sect. 1. *Campylosporus*) or *H. styphelioides* (sect. 29. *Brathys*) (Fig. 9f), there may be up to eight main lateral veins, but the venation is advanced in other respects relative to that of *H. bequaertii* in that these lateral veins are branched.

With the proviso, then, that *H. bequaertii* may be specialised relative to some other species in the number of its basal veins, it may be taken as the basic species from which to show trends in major leaf-venation in the genus (Fig. 10a). These trends involve (i) adnation of the basal veins to the midrib (e.g. in *H. quartinianum, H. hirsutum*) (Fig. 10h, r), (ii) pinnation of the midrib (e.g. in *H. revolutum, H. brasiliense*) (Fig. 10b, c, z), (iii) incurving of vein ends to form an intramarginal vein (e.g. in *H. roeperanum, H. frondosum*) (Fig. 10i, k), (iv) condensation of the lower part of the midrib, so that the main lateral veins radiate from one point (e.g. in *H. elodes, H. mutilum*) (Fig. 10n, b′), (v) elimination of some or all basal veins so that eventually only an intramarginal vein remains (e.g. in *H. balearicum, H. scopulorum*) (Fig. 10e, p) and (vi) reticulation, i.e. the in-filling of spaces between main veins or laterals with increasingly dense reticulate venation (e.g. in *H. androsaemum, H. frondosum*) (not shown in Fig. 10). Two further points relating to Fig. 10 should be noted: (i) reduction trends resulting in the elimination of all veins except the midrib occur in other sections besides 29. *Brathys* (e.g. in sects 17, 18, 26, 30), but only where an intramarginal vein has *not* formed; (ii) an apparent increase in the number of basal veins is sometimes (? always) due to branching (e.g. in some plants of *H. elatoides*) (Fig. 10x).

(*c*) *Glandularity*

The glandular pattern in the leaves is, in part, intimately connected with that of the venation, and so it is appropriate to discuss it here.

There are two types of gland present in the leaves of *Hypericum*: (i) Blackish or red clusters of cells containing a wax impregnated with hypericin (a dianthrone) or occasionally pseudohypericin, and (ii) schizogenous intercellular spaces lined by cells which secrete a translucent essential oil (Coutinho, 1950; Mathis, 1963; Mathis & Ourisson, 1963, 1964*a*, *b*). These can conveniently be called 'dark' and 'pale' glands, respectively. Pale glands are present in all species (Green, 1884), although they may not be visible externally in some heavily sclerotinized or cutinized leaves; but dark glands are sometimes completely absent from the plant or confined to organs other than the leaves, and this variation in occurrence has been used in the classification of the genus (Clos, 1868; Siersch, 1927; Roth, 1953; Mathis & Ourisson, 1963) (see p. 149).

The pale glands are also of two types that have quite distinct evolutionary origins:

(i) As we have shown already, the main veins in *H. bequaertii*, *H. revolutum* subsp. *keniense* and *H. lanceolatum* subsp. *angustifolium* are interspersed with weaker, dichotomising, apparently functionless veins (Figs 9e, 11a) which appear to have evolved by differentiation from an equal-veined flabellate condition (Fig. 9). With branching of the midrib and secondary veins the course of these functionless veins (which have become linear 'pale glands') has been interrupted (Fig. 11b), and formation of increasingly denser tertiary reticulate venation has resulted first in glandular streaks and then isodiametric glands e.g. in *H. roeperanum* or *H. revolutum* subsp. *revolutum* (Figs 9, 11).

(ii) Interspersed with the veins and vein-glands in *H. bequaertii* are irregular rows of small pale glandular dots (Fig. 11a). These glands do not seem to correspond to any structures in other subfamilies of the Guttiferae, but the glands in *Santomasia* and the Vismieae appear to be homologous with them. The pale glands in the Cratoxyleae, however, seem to have had an origin like those in type (i) of *Hypericum*. Glands of type (ii) are present in sect. 1. *Campylosporus* only in *H. bequaertii, H. revolutum* subsp. *keniense* and *H. lanceolatum* subsp. *angustifolium*. It is the only type to occur in sects 29. *Brathys* and 30. *Spachium*, the

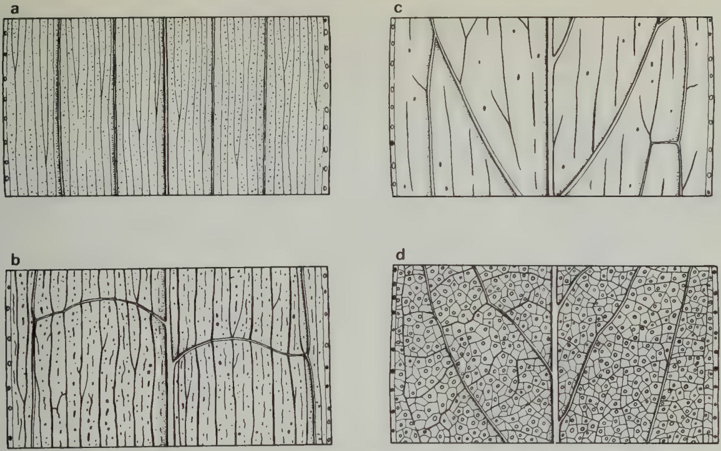

Fig. 11 One origin of pale glands in leaves of *Hypericum*: (a) *H. bequaertii* (x 6); (b) *H. revolutum* subsp. *keniense* (x 12); (c) *H. revolutum* subsp. *revolutum* (x 12); (d) *H. roeperanum* (x 4).

functionless veins having apparently disappeared completely during the evolution of these sections or, in *Brathys*, perhaps they never evolved; and glands of this type are present in some species of sect. 3. *Ascyreia* as small, superficial dots. All other pale glands in the leaves of *Hypericum* are derivatives of the functionless veins (i.e. type (i)).

The dark glands are associated particularly with the leaf margins and the region immediately interior to them, and Green (1884) pointed out that they were 'in intimate relationship with the fibrovascular system'. This is true of only the more primitive species. In other parts of the genus there are 'laminar' as well as 'marginal' dark glands; and these develop in positions which, in related species, are occupied by pale glands. There is no doubt, however, that Green's observation is partially valid; and a comparison with the Bonnetioideae confirms its validity. In *Ploiarium alternifolium* (Vahl) Melchior and *Bonnetia stricta* (Nees) Nees & Martius, for example, the leaf margins have indentations towards the apex each containing a sessile gland or gland-tooth which terminates a vascular strand. In the leaves of species of *Hypericum* sect. 1. *Campylosporus* there are comparable glands, but these do not interrupt the contour of the margin; they are thus marginal or (when more deeply imbedded) inframarginal or submarginal. In *H. bequaertii* they are amber in colour and therefore contain no hypericin, only the wax base; but in some other species (e.g. *H. roeperanum*) they are reddish or dark due to their hypericin content.

As was mentioned above, this variability in the strength and occurrence of hypericin can be used to characterise sections or large parts of the genus (Fig. 12; Robson, 1977*a* : fig. 1). For example, in sect. 3. *Ascyreia* and some of its derivatives (sects 4, 5, 7), red or black glands are totally absent. In sects 6. *Inodorum* and 8. *Bupleuroides* they are sometimes present on sepal margins only, and then usually only reddish. In the *Hirtella* group (sects 17–19) they are usually only marginal in the perianth and usually either absent from the leaves or apical or laminar, not marginal. They may, however, occur on the stem. In the *Olympia* group (sects 10–16) they are marginal and often also laminar in the leaves and perianth but do not occur on the stem; whilst in sect. 9. *Hypericum* they are similarly distributed but do also occur on the stem.

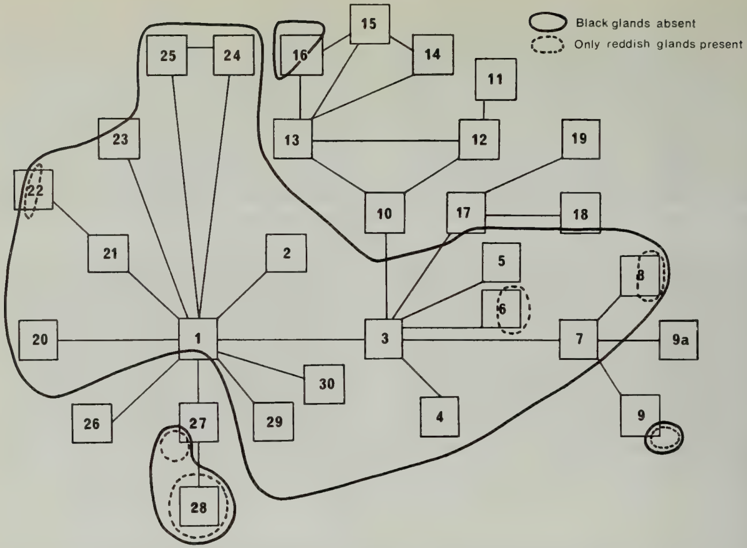

Fig. 12 Variation in distribution of black or reddish glands in *Hypericum.*

On the other hand, related species may differ widely in the occurrence of hypericin. In sect. 27. *Adenosepalum* black glands are numerous and widespread in the more primitive species; but in the apparently derived sect. 28. *Elodes* the glands are usually merely reddish and confined to the sepal margins. A similar diminution in hypericin content is shown in the eastern Himalayan members of sect. 9. *Hypericum*, which are derived from a group of Chinese species with dark glands. An even more vivid example is found in sect. 16. *Crossophyllum*, where, of the two species (both with gland-fringed leaves), *H. adenotrichum* has dark marginal and superficial glands, whereas in *H. orientale* all the glands are pale (not even reddish). In the Vismieae, *only* amber to dark glands are present, whereas the Cratoxyleae have only pale glands.

Inflorescence

(*a*) *Form*

As in the Bonnetiaceae, the inflorescence in *Hypericum* is basically cymose; but it never has a truly axillary position, i.e. in the axils of foliage leaves with the terminal bud remaining

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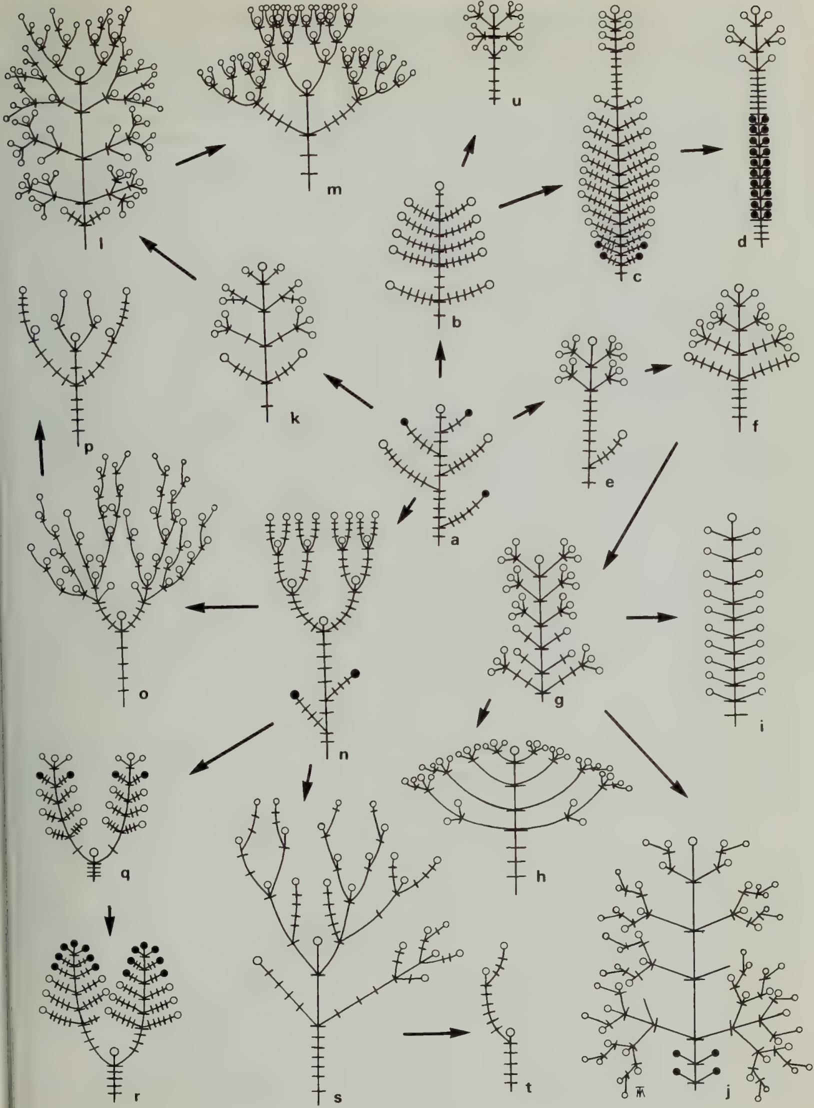
Fig. 13 Trends in inflorescence-branching in *Hypericum* (numbers indicate sections): (a) *H. bequaertii* (1); (b) *H. revolutum* (1); (c) *H. aegypticum* (25); (d) *H. heterophyllum* (24); (e) *H. quartinianum* (1); (f) *H. roeperanum* (1); (g) *H. cordifolium* (3); (h) *H. scabrum* (17); (i) *H. salsolifolium* (17); (j) *H. punctatum* (9); (k) *H. brasiliense* (30); (l) *H. laxiusculum* (30); (m) *H. myrianthum* (30); (n) *H. styphelioides* (29); (o) *H. chamaemyrtus* (30); (p) *H. diosmoides* (30); (q) *H. carinosum* (29); (r) *H. thuyoides* (29); (s) *H. natalense* (26); (t) *H. peplidifolium* (26); (u) *H. tortuosum* (23). ○ Flower, ● bud.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vegetative (as in *Ploiarium* or *Neogleasonia*). The most primitive inflorescence in *Hypericum* is 1-flowered, as it is in *Kielmeyera*, for example; and the opposite decussate phyllotaxis results in elaboration by formation of dichasia or pseudo-dichotomies. These dichasia, sooner or later and to differing degrees in various sections, give way to monochasia. Reduction can, of course, set in at any evolutionary stage, the dichasia being replaced by single flowers. Although the branching is basically cymose at the level of the inflorescence, so that laterals do not develop until the terminal flower is initiated, in the young plant of e.g. *H. revolutum* (sect. 1) they appear long before that event. The main shoot at that stage is therefore indeterminate (hapaxanthic); and the 'architecture' of the branching would seem to conform with the type described as Scarrone's Model by Hallé, Oldeman & Tomlinson (1978):

> 'The architecture is determined by an orthotropic rhythmically active terminal meristem which produces an indeterminate trunk bearing tiers of branches, each branch-complex orthotropic and sympodially branched as a result of terminal flowering.'

The terminal bud (always?) eventually forms a flower, and then the 'single trunk' form gives way to a 'bush' form. Development of shoots from the base of the main stem (i.e. basitony sensu Hallé, Oldeman & Tomlinson, 1978) is common and contributes to the aspect of many species.

The basic state of branching at the flowering level is well shown in *H. bequaertii* (Fig. 13a). Below the terminal solitary flower are one or more nodes in which branch development is absent, presumably having been inhibited by hormones from the apical meristem. Along the remaining length of stem a varying number of branches are produced, the most advanced ones being somewhere in the middle (i.e. immediately below the inhibitory zone).

Two of the three major trends in elaboration of the inflorescence are discernible in sect. 1. *Campylosporus*: (1) In e.g. *H. revolutum* and *H. madagascariense* the central, branching zone becomes continuous (i.e. all nodes have branches), but the branches remain 1-flowered (Fig. 13b). (2) In e.g. *H. quartinianum*, on the other hand, the uppermost node(s) produce single flowers or triads (Stauffer, 1963), there being usually a non-branching zone between these and the uppermost flowering branches (Fig. 13e). In *H. roeperanum* this non-branching zone is absent and there is a continuous progression from terminal flower, through lateral flowers, triads (1-noded inflorescence branches) and paracladia (2-or-more-noded inflorescence branches), to the uppermost flowering branch (where the inflorescence module is repeated on a reduced scale, in this example reduced to a single flower) (Fig. 13f). The paracladia may bear triads only, or the subterminal node(s) may also be fertile. (3) The third major trend in inflorescence elaboration can be described as pseudo-dichotomy (Fig. 13n), in that both axillary buds of the terminal node (below the flower) produce branches, not dichasia. If the flower falls, as it does in *H. styphelioides*, for example, the resultant effect is of repeated dichotomized branching. The occurrence of pseudo-dichotomy is confined to only four sections: 20. *Myriandra*, 26. *Humifusoideum*, 29. *Brathys* and 30. *Spachium*.

All *Hypericum* inflorescences can thus be described in terms of modification of (i) the terminal flower and the nodes immediately beneath it and (ii) the intermediate zone of 1-flowered branches, i.e. whether the terminal elaboration is dichasial or pseudo-dichotomous, and whether or not the intermediate zone is present. To these two modifications, which may be termed respectively acrotonal and intercalary, must be added a third (basitonal), in that the nodes occupied by the inflorescence proper (i.e. terminal flower, dichasia and paracladia) may increase in number basipetally (Figs 13c, e) until eventually the non-branching zone is eliminated (Fig. 13f). Where this has occurred, it may be impossible to differentiate paracladia from lateral branches (cf. Stauffer, 1963). Basitony combined with reduction of the dichasia to single flowers results in a spike, e.g. in *H. geminiflorum* (sect. 4. *Takasagoya*) or *H. salsolifolium* (sect. 18. *Hirtella*) (Fig. 13i).

Dichasial to monochasial branching is the only type of acrotony that occurs in sect. 3. *Ascyreia* and its derivatives (sects 4–19), and also in sects 20–25, 27. *Adenosepalum* and 28. *Elodes* (Fig. 13c-j). In some species (e.g. in sect. 30. *Spachium,* Fig. 13m), dichasia of up to the 4th order may be produced before monochasium-formation sets in. In others (e.g. in sect. 9. *Hypericum,* Fig. 13j) it sets in after the appearance of the 2nd-order flowers.

Dichasium-formation is rare in sect. 29. *Brathys* (occurring, for example, in *H. phellos*, *H. pseudocaracasanum* and *H. humboldtianum*), and the dichasia are never elaborate. The primitive type of branching in this section is pseudo-dichotomy (e.g. in *H. styphelioides*, Fig. 13n); and, where this is the sole type of branching (e.g. in *H. bryoides*), a dense rounded shrub is formed, approximating to Leeuwenberg's Model (Hallé, Oldeman & Tomlinson, 1978). In this section, further evolution has mainly been by elaboration of the intercalary zone (e.g. in *H. carinosum* or *H. phellos,* Fig. 13q), leading eventually in *H. laricifolium* and its relatives to retarded development of the inflorescence proper (i.e. the terminal flower) and the conversion of the shoot from determinate to indeterminate growth (Fig. 13r). In sects 20. *Myriandra*, 26. *Humifusoideum* and 30. *Spachium* both types of branching are found, sometimes in the same inflorescence ('mixed inflorescence') (Fig. 13o, p, s).

Another cause of differences in inflorescence size, though not in complexity, is variation in the length of the internodes. Extreme condensation produces a subumbellate corymb, e.g. in *H. scabrum* (sect. 17. *Hirtella*) (Fig. 13h); elongation may result in a candelabra-like form (e.g. in *H. monogynum* and its relatives, sect. 3. *Ascyreia*).

Extreme reduction can result in either the elimination of branches, producing a secondarily 1-flowered inflorescence (e.g. *H. nummularium*, sect. 19. *Taeniocarpium*, or forms of *H. anagalloides*, sect. 30. *Spachium*), or sterilisation (i.e. delayed development) of lateral branches (as in *H. heterophyllum*, sect. 24. *Heterophylla*) (Fig. 13d). In some species (e.g. *H. peplidifolium*, sect. 26. *Humifusoideum*; *H. elodes*, sect. 28. *Elodes*; *H. scioanum*, sect. 30. *Spachium*), development of only one of the pair of axillary buds at the terminal node results in sympodial branching and apparently lateral inflorescences (Fig. 13t). As regards elaboration, inflorescence branches always arise singly, except in *H. laxiusculum* (sect. 30. *Spachium*), where accessory branches occasionally occur at the terminal node (cf. St Hilaire, 1824–1828 : t. 61).

In conclusion, which method of acrotonal branching seems to be 'the most primitive'? In most parts of the genus the elaboration is in the order: single flower—dichasium—monochasium, or, where mixed inflorescences occur: single flower—pseudo-dichotomy—dichasium—monochasium. In sect. 29. *Brathys*, however, the single-flower stage is rare and, as stated above, dichasium-formation is rarely present and then rudimentary. Nevertheless, we should conclude that, here too, the pseudo-dichotomous inflorescence is derived.

(*b*) *Bracts and bracteoles*

In *Hypericum bequaertii* the transition in form from leaf to sepal is sudden, the uppermost leaves being only a little smaller than the others; and wherever the inflorescence is 1-flowered, the same tends to be true. For example, most species of sect. 29. *Brathys* show this sudden transition, only a few having upper leaves intermediate in form.

In more complex inflorescences and their derivative forms, however, the bracts (uppermost leaf pair) and bracteoles tend to be more similar to the sepals than to the leaves, i.e. the sudden transition is often from the leaves to the bracts. This resemblance to the sepals extends to glandularity. In general, the bracts and bracteoles are persistent for at least as long as the leaves, i.e. where the leaf-base is articulated (see p. 76), the bracts and bracteoles tend to be deciduous; but in sects 3. *Ascyreia* and 4. *Takasogoya* they are caducous.

In sects 15. *Thasia* and 16. *Crossophyllum*, and also, independently, in sect. 27. *Adenosepalum*, the basipetal extension of sepaline characters has penetrated beyond the inflorescence into the foliage leaves. In some African species of sect. *Adenosepalum* (e.g. *H. annulatum*), the sepals and bracts are gland-fringed, and at the base of the bracts the glandular cilia form auricle-like clusters; whereas, in the most closely related Asian species (*H. elodeoides*, *H. himalaicum*, *H. wightianum*), the upper leaves also usually have glandular fringes and glandular auricles. Likewise, in sect. *Thasia* the upper leaves have glandular fringes and auricles; but in sect. *Crossophyllum* all the leaves are gland-fringed and have true auricles, not merely clusters of glandular cilia (see p. 76).

Sepals

(*a*) *Insertion and number*

The transition from the opposite decussate phyllotaxis of the leaves to the 2/5 spiral (quincuncial) phyllotaxis of the calyx appears to be relatively sudden in most species of *Hypericum*, in that the upper leaves and bracts are usually opposite. Occasionally, however, the bracteoles or upper leaves are not strictly opposite, e.g. in *H. tomentosum* (Wydler, 1851), or one of the bracts may be absent (Wydler, 1859, 1871). This tendency towards merging of the phyllotactic systems never becomes a permanent feature in *Hypericum*, whereas in some west African species of *Psorospermum* (*P. alternifolium* J. D. Hook., *P. guineense* (L.) Hochr., *P. corymbiferum* Hochr. and *P. lanatum* Hochr.) the upper leaves and branches are constantly alternate to spiral. A comparison of these species with the rest of the Vismieae indicates that this is an advanced state, not one transitional from the spiral phyllotaxis typical of most Bonnetioideae and the Theaceae to the opposite decussate arrangement typical of the rest of the Guttiferae.

The suddenness of the transition from opposite to quincuncial insertion in *Hypericum* is, however, often more apparent than real. In the large, regularly pentamerous flowers of sect. 3. *Ascyreia*, the two outermost sepals (1 and 2) do not diverge by the ideal 2/5 angle of 144°, but by one that averages 180°. Breindl (1934) records a range of 160°–200° for '*H. hookerianum*'. Likewise, sepals 3 and 4 are only about 20° divergent from the opposite position in this species (161°–199° in one flower measured). It is only by adding together the divergence angles of each pair that space can be provided for sepal 5, which diverges from sepal 3 by only 54°, not by the ideal 72°. These spatial relationships are reflected in temporal ones, in that the almost opposite pairs of sepals arise nearly simultaneously, i.e. 1–2, 3–4, 5 (cf. discussion below under 6. Development, p. 125). In flowers with meiomerous inner whorls the angle between sepals 1 and 2 tends to become larger, and sepals 3, 4 and 5 then arise together, i.e. the order is 1–2, 3–4–5.

These trends in spatial and temporal relationships of the sepals explain how there is a tendency towards crowding in the inner floral whorls, with consequent elimination of the gynoecial members on the radii of sepals 5 and frequently 4, and the fusion of androecial members on either side of these radii (see Fig. 21, p. 104). This tendency occasionally extends to the perianth in sections where this is normally pentamerous, e.g. in *H. humifusum* (sect. 14. *Oligostema*) (Martin-Sans, 1922) or in some populations of *H. monanthemum* Hook.f. & Thomson ex Dyer from Sikkim and Nepal, which were described as *Ascyrum filicaule* by Dyer (1874).* The tendency towards tetramery is most marked, however, in sect. 20. *Myriandra*, where several species have a constantly tetramerous perianth and androecium and comprise the Linnaean 'genus' *Ascyrum* (Robson, 1977*a*, 1980*c*). Transitional conditions are found in this section, for example in *H. frondosum*, where the sepals are often foliaceous and the calyx and corolla may vary from pentamerous to tetramerous on one plant. In all the typically tetramerous species except *H. microsepalum* (which is not closely related to them, see Figs 4, 5), the elimination of sepal 5 has been followed by differentiation of the remaining ones into a larger outer pair and a smaller inner pair, these pairs being of course at right angles to one another. In *H. hypericoides* the smaller, inner pair is sometimes obsolete (i.e. vestigial) (fide Adams 1957).

An example of an apparently opposite trend is found in the prostrate, few-flowered form of *H. empetrifolium* (sect. 19. *Coridium*) that is known horticulturally as var. *prostratum* (correctly var. *oliganthum* K. H. Rech.). In it the influence of the 3-whorled phyllotaxis has

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*In the first paper of this series (Robson, 1977*a*), *Hypericum filicaule* (Dyer) N. Robson was considered to be distinct from *H. monanthemum*. Further work has shown these taxa to be conspecific and to belong to sect. 9. *Hypericum*, not to sect. 27. *Adenosepalum*.

been carried over to the perianth, which is hexamerous. In both calyx and corolla the irregular disposition of the members indicates that an extra member has been 'added on'. There is no evidence of true trimery. Wydler (1878) found comparable variation in the flowers of *H. coris*, another species of sect. *Coridium*.

(*b*) *Relative size, shape, union and persistence*

The difference in size between inner and outer sepals in species with a tetramerous perianth (e.g. *Hypericum hypericoides*) is an extreme manifestation of a general tendency in parts of the genus towards inequality in sepal size—a tendency that is associated with the spatial and temporal relationships discussed above. The most primitive condition, as shown in *H. bequaertii* and its near relatives, is slight inequality, the inner sepals being usually somewhat smaller than the outer ones, with sepal 3 intermediate in size.

In some sections (e.g. 17. *Hirtella*) there is a tendency towards equality (e.g. in *H. scabrum*), whereas in others the tendency is in the opposite direction. Foliaceous or very unequal sepals have evolved repeatedly, e.g. in sect. 3. *Ascyreia* (*H. calycinum*, *H. prattii*, *H. choisianum*), sect. 5. *Androsaemum* (*H. androsaemum*), sect. 7. *Roscyna* (*H. przewalskii*) and sect. 14. *Oligostema (H. humifusum*). The evolution of markedly unequal sepals is usually accompanied by a tendency towards their spreading or reflexing in bud and/or fruit, but these developments are associated with no obvious biological changes related, for example, to pollination or dispersal.

Sepal shape is extremely variable and shows no general trends, although narrowness is usually relatively advanced. There is, however, a trend towards union of the sepals, which are primitively quite free at the base. In the most extreme forms, e.g. in *H. cardiophyllum* (sect. 22. *Arthrophyllum*), *H. kotschyanum* (sect. 18. *Taeniocarpium*) or *H. scabrum* (sect. 17. *Hirtella*), the sepals may be up to 2/3 united; but in most species they are free or united only at the base. Union is not particularly associated with the development of pseudotubular flowers and specialised insect pollination (in sects 25. *Adenotrias* and 28. *Elodes*), as the sepals are free in the former and 2/5 united in the latter. Whether united or not, the imbricate quincuncial arrangement is always visible in bud, although in calyces with relatively narrow sepals the aestivation at the base may be almost open, e.g. in *H. brachyphyllum* (sect. 20. *Myriandra*).

In most *Hypericum* species the sepals persist during and after development of the fruit; but in two separate sections they are sometimes deciduous. In sect. 5. *Androsaemum* they are persistent in all except *H. hircinum*, even in its hybrid with *H. androsaemum* (*H.* x *inodorum* Miller). In sect. 20. *Myriandra*, however, the sepals are primitively deciduous after fruit dehiscence (i.e. in subsect. *Myriandra*) but become persistent again in all but one of the derivative herbaceous or tetramerous species (subsect. *Pseudobrathydium* R. Keller) (cf. Adams, 1962*a*).

(*c*) *Vestiture*

Only the outer surface of the sepals ever has an indumentum, and that resembles the vestiture of the corresponding vegetative parts. There are no species in which hairs are confined to the sepals; but in *H. reflexum* and *H. annulatum* (sect. 27. *Adenosepalum*) or *H. setosum* (sect. 30. *Spachium*), for example, the vegetative parts are wholly or partly indumentum-covered, whereas the sepals are glabrous.

(*d*) *Venation*

The sepals in *Hypericum* are basically 3-trace organs (see p. 129). The three traces may depart from the same stelar gap (Fig. 32, p. 129); but more usually there are three gaps, with the laterals of adjacent sepals (often united initially) departing from the same gap (Fig. 35, p. 131). The three traces then dichotomise several times in the base of the sepal or not, depending on its width, so that the sepal has one to many veins, parallel or diverging (Fig.

14). In the more primitive and many relatively advanced species, further branching is also dichotomous (e.g. *H. roeperanum*, sect. 1. *Campylosporus*, Fig. 14a), but pinnation often occurs, especially towards the margin (e.g. in species of sect. 9. *Hypericum*, where it is accompanied by the looping of the laterals on to the midrib or on to each other, Fig. 14b). In foliaceous sepals (e.g. in *H. przewalskii*, Fig. 14c) a densely reticulate venation is produced; but this is always clearly a development from parallel or diverging veins, unlike the reticulation in the leaves, which tends to develop from midrib branches (cf. Fig. 10). Thus, in general (and for any given species) the venation of the sepals is at a less advanced stage of evolution than is that of the leaves. Where the sepals are narrow, however, the laterals and branchings may be few or absent, as in narrow leaves (Figs 10h, 14d).

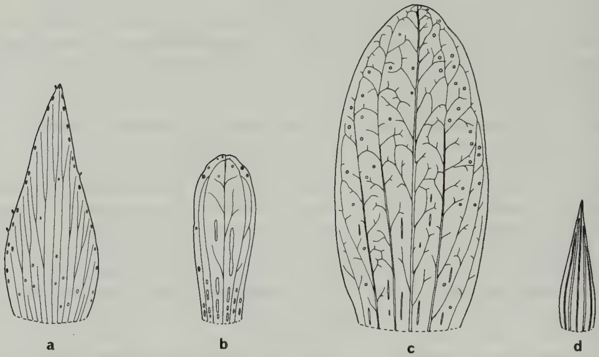

Fig. 14 Variation in sepal venation in *Hypericum*: (a) *H. roeperanum*; (b) *H. sampsonii*; (c) *H. przewalskii*, (d) *H. brathys* (all x 6).

(*e*) *Margin*

Like the sepal margins of the Bonnetioid genera, that of *Hypericum* is primitively entire (Figs 15a, 16); but sect. 1. *Campylosporus* contains species in which it is gland-fringed (Fig. 15b), and even in *H. bequaertii* it sometimes has minute eglandular denticles. These do not appear to be associated with vein-endings. In some sections the margin remains constantly entire (e.g. in 5. *Androsaemum*, 20. *Myriandra*, 29. *Brathys*) (Fig. 15u, y), whilst in others it is constantly fringed (e.g. in 13. *Drosocarpium*, 19. *Coridium*) (Fig. 15h, i); but in several sections both conditions are found (e.g. in 9. *Hypericum*, 17. *Hirtella*) (Fig. 15e, r), and the change from entire to fringed seems to have occurred independently in most of them (Fig. 16). Although this change is usually associated with the emergence of marginal glands, in some sections an eglandular eroded-denticulate margin has developed (e.g. in 3. *Ascyreia*, 9. *Hypericum*, 30. *Spachium*) (Fig. 15c, f). In general, an entire sepal margin is a primitive character, but there has been a reversion from gland-fringed to entire sepals in at least four sections: 9. *Hypericum* (*H. monanthemum*), 11. *Campylopus* (*H. cerastoides*), 14. *Oligostema* (*H. australe*, *H. humifusum* pro parte) and 27. *Adenosepalum* (e.g. *H. himalaicum* N. Robson = *H. humifusum* sensu Dyer non L.) (cf. Fig. 15j, k). In some sections (e.g. 1. *Campylosporus*) the denticles precede the glands (i.e. in these sections they are primitively eglandular), whereas in others (e.g. *Webbia*) (Fig. 15v) the emergences are glandiferous from the beginning.

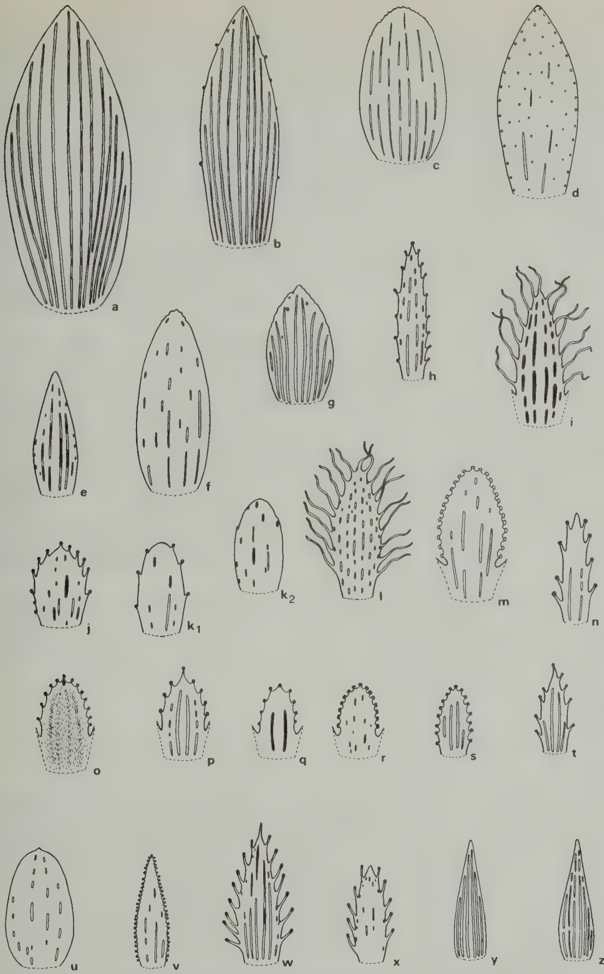

Fig. 15 Variation in marginal contour and in glandularity of sepals in *Hypericum* (numbers indicate sections): (a) *H. bequaertii* (1); (b) *H. quartinianum* (1); (c) *H. forrestii* (3); (d) *H. formosanum* (4); (e) *H. erectum* (9); (f) *H. maculatum* subsp. *obtusiusculum* (9); (g) *H. polyphyllum* subsp. *polyphyllum* (10); (h) *H. montbretii* (13); (i) *H. barbatum* (13); (j) *H. linarifolium* (14); (k) *H. humifusum* (14); (l) *H. thasium* (15); (m) *H. orientale* (16); (n) *H. hirtellum* (17); (o) *H. salsolifolium* (17); (p) *H. uniglandulosum* (17); (q) *H. retusum* (17); (r) *H. asperulum* (17); (s) *H. pumilio* (18); (t) *H. fragile* (18); (u) *H. prolificum* (20); (v) *H. canariense* (21); (w) *H. elodeoides* (27); (x) *H. wightianum* (27); (y) *H. strictum* (29); (z) *H. brasiliense* (30) (all x 5).

(*f*) *Glandularity*

The sepals bear the same types of gland as do the leaves, viz. (i) black or red cell-clusters containing hypericin and (ii) schizogenous pale punctiform or elongate lacunae containing essential oils. The occurrence and form of these glands vary in different parts of the sepal, which can be divided into four regions: (i) laminar—not associated with the margin; (ii) submarginal—towards the margin; (iii) inframarginal—immediately below the margin but not breaking the line of it; (iv) marginal—breaking the line of the margin. The various types of gland are homologous with those in similar positions in the leaves, the bracts and bracteoles, as already stated, being intermediate in glandularity between leaf and sepal.

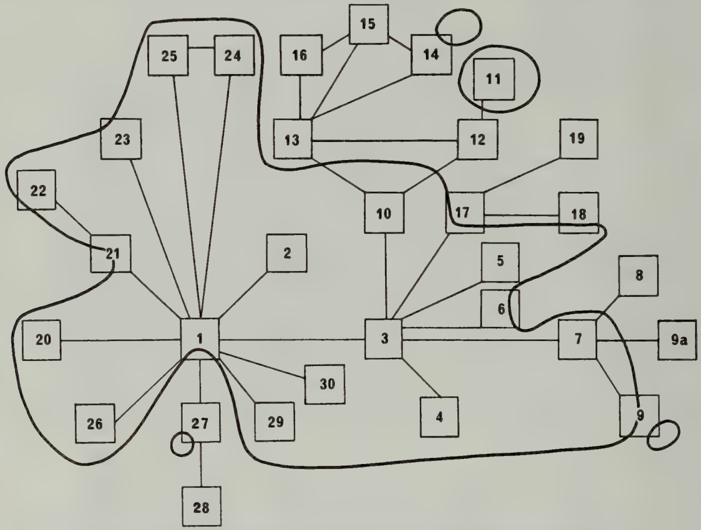

Fig. 16 Distribution of entire sepal margin in *Hypericum* (within line).

(i) Laminar. As was observed above with regard to venation, so it is with laminar glands: the sepals in general show a less advanced state than do the leaves, i.e. they retain pale glandular lines (canals) for longer. Thus, in a given species the chances are that, if the laminar pale glands of the leaf are dots or streaks, those of the sepals are at least partly linear.

Although these glandular lines occur between the veins, as in the primitive leaves, nevertheless they do not appear to have a relation to functionless veins. Nor is their dissection apparently related to increasingly reticulate venation, as the lines are frequently discontinuous towards the margin when the veins are not or scarcely branched. There is nevertheless a trend from almost unbroken lines* in the primitive sections (and *Santomasia*) to increasing distal and marginal dissection, culminating in sepals with punctate or shortly elongate glands only, e.g. in *Hypericum thasium* (sect. 15. *Thasia*) (Fig. 15l) and *H. wightianum* (sect. 27. *Adenosepalum*) (Fig. 15x).

The dark laminar glands, like those of the leaf lamina, occur in positions which correspond to those of pale glands in related species or sections. Thus, whereas the sepals in many species of sect. 17. *Hirtella* have two pale linear glands, in *H. retusum* these are replaced by two dark linear glands, and in *H. asperulum* they are dark streaks or dots (Fig. 15q, r). The replacement may be incomplete, so that a linear gland is mostly pale but has dark sections (e.g. in forms of *H. erectum*, sect. 9. *Hypericum* or *H. elodeoides*, sect. 27. *Adenosepalum*) (Fig. 15e, w). Although direct replacement of pale line by dark line can therefore occur, the trend in dark glands is more usually from dots to lines by means of linear extension or coalescence.

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*Where the sepals are thick, the lines, though continuous, may appear broken (cf. Fig. 14a).

(ii) Submarginal. In many species the dark glands towards the margin are punctiform whilst those nearer the midrib and base are longer. But a few species have a definite row of dark dots or short streaks which, while not touching the margin, are associated with it. These seem to be confined to sect. 1. *Campylosporus* (*Hypericum revolutum*, *H. gniidfolium*, *H. lanceolatum*, *H. madagascariense*, *H. quartinianum*, *H. roeperanum*) (Fig. 15b), although in *H. polyphyllum* (sect. 10. *Olympia*) they approach the submarginal position (Fig. 15g). As they are merely dark distal portions of otherwise pale glands, these submarginal glands are really only a special type of laminar gland.

(iii) Inframarginal. The inframarginal glands, on the other hand, are a special type of marginal gland that is associated with entire sepals, whereas marginal glands (by definition) occur on an interrupted sepal margin. Indeed both types may occur in the same species (e.g. *Hypericum humifusum*) (Fig. 15k). In at least two species (*H. thasium*, sect. 15. *Thasia* and *H. wightianum*, sect. 26. *Adenosepalum*) inframarginal and stipitate marginal dark glands appear to occur on the same sepal, both species having sepals with glandular or eglandular fimbriae between which are dark glandular dots that break the line of the margin (Fig. 15l, x). By comparison with related species (respectively *H. montbretii* and *H. elodeoides*) (Fig. 15h, w), however, it is clear that these are laminar glands that appear to have become marginal due to the deep incision of the margin.

Inframarginal sepal glands, like inframarginal leaf glands, are always punctiform or elliptic, never more elongated.

(iv) Marginal. Whereas the laminar and submarginal glands obviously develop *between* the veins, there has been disagreement about the relative position of the marginal and inframarginal ones. Clos (1868) stated that the 'marginal' (i.e. non-stipitate) glands occur between the veins, whilst the glandular cilia appear at the ends of the veins; but Green (1884) described both as being 'in intimate relationship with the fibrovascular system.' My observations lead me to agree with Clos that the association with veins occurs only in stipitate glands. But it does not always occur. In species where the marginal glands are primitively small (and often reddish rather than dark, e.g. in *Hypericum revolutum*, sect. 1. *Campylosporus* or *H. canariense*, sect. 21. *Webbia* (Fig. 15v)), there is no association with the vascular system. Nor is there any vascular connection with the eglandular marginal denticles in, for example, *H. forrestii* (sect. 3. *Ascyreia*) and *H. maculatum* subsp. *obtusiusculum* (Tourlet) Hayek (sect. 9. *Hypericum*) (Fig. 15c, f). It would seem, therefore, that the marginal accumulation of glandular material is the primary phenomenon, the association with the vascular system being a secondary one.

The trend from inframarginal via marginal to stipitate glands is reversible. Thus, in sect. 14. *Oligostema*, *H. linarifolium* has subequal sepals with ciliate margins comparable with those of the most closely related species in sect. 12. *Origanifolia*—and indeed with most species in sects 12–16 (Fig. 15j). The cilia mostly contain a vascular strand. In the very closely related *H. australe* and *H. humifusum* (Fig. 15k), the sepals tend to be entire and (particularly in *H. humifusum*) unequal, when the glands revert to the inframarginal position with no vascular connection.

The distribution of dark glands, as we have already seen, can be used as a taxonomic character (p. 80; Robson, 1977*a*). In some sections the sepals have no dark glands (e.g. 2–5, 7, 20, 24, 25, 29, 30), in some they are small and rudimentary (6, 8, 21), in others they are sometimes present (1, 22, 23), and in the remainder they are constantly present (9–19, 26–28). The dark glands may occur alone, but dark laminar glands are nearly always accompanied by dark marginal ones. An exception to this rule occurs in sect. 10. *Olympia*, where the entire sepals of *H. polyphyllum* are without marginal glands but usually have laminar dark glands (Robson, 1967*a*, *b*, 1980*b*) (Fig. 15g).

Marginal dark glands first appear either as small, sessile, reddish or blackish, globose structures (sects 6, 8, 17, 18, 21) or as minute amber to blackish denticles (sect. 1). In more advanced stages of evolution they may terminate glandular cilia (short, spreading, not interrupting the marginal line), glandular denticuli (short, ascending, not interrupting the marginal line), glandular fimbriae (long, spreading, not interrupting the marginal line) or glandular laciniae (long, spreading or ascending, interrupting the marginal line). In some more advanced species the emergences become eglandular (e.g. in *H. barbatum*, sect. 13. *Drosocarpium* and *H. thasium*, sect. 15. *Thasia*) (Fig. 15i, l), or the glands may lose some or all of their hypericin and become red (e.g. in *H. elodes*, sect. 28. *Elodes*) or amber (e.g. in *H. orientale*, sect. 16. *Crossophyllum*) (Fig. 15m). The shape of the stipitate glands also varies. They are usually globose or ellipsoid; but obconic ones occur in sects. 9. *Hypericum* (e.g. *H. monanthemum*), 17. *Hirtella* (e.g. *H. hirtellum*) (Fig. 15n) and 27. *Adenosepalum* (e.g. *H. annulatum*); and, at least in sect. *Hirtella*, this difference in shape can be of taxonomic importance (Robson, 1967*c*, 1968).

What appears to be a special type of marginal dark gland occurs in sects 17. *Hirtella* and 18. *Taeniocarpium*, sections in which such glands are normally absent from the leaves. In sect. *Hirtella*, the upper leaves and sometimes the sepals of *H. salsolifolium* (Fig. 15o) have a subapical or apical more-or-less irregular accumulation of dark glandular material, the apical mucro of the leaf being eglandular; whilst in the closely related *H. uniglandulosum* (Fig. 15p), where both leaf and sepal are mucronate, the subapical gland is absent, but the mucro is often glandiferous. In sect. *Taenocarpium*, the leaves (but not the sepals) of *H. nummularium* have two conspicuous apical dark glands, which in the taxonomically adjacent *H. monadenum* have united to form one large gland. Other species of this affinity have 1–5 small apical leaf glands (*H. pumilio*) (Fig. 15s) or none (*H. nummularioides*, *H. fragile*, *H. saxifragum*) (Fig. 15t). In the taxonomically somewhat isolated *H. haplophylloides*, an Albanian endemic species which comprises two disjunct populations, whereas both subspecies have apical dark glands in the leaf, only one (subsp. *devollense* F. K. Meyer) has sepals with a glandiferous apex (Meyer, 1978).

Petals

(*a*) *Insertion and number*

Whereas the phyllotaxis of the leaves and the perianth of the Dilleniaceae and Theaceae are constantly spiral, the Guttiferae show transitions to whorled phyllotaxis in both regions. But, whilst the transition in leaf-insertion is apparent in the Guttiferae only in the Bonnetioideae, as we have seen (p. 73), that in the perianth is more widespread. In transitional stages of perianth aestivation, instead of having two organs wholly exterior, two wholly interior and one (no. 3) half exterior and half interior (Fig. 17a), there are fewer wholly exterior or interior and more in the half-and-half position characteristic of the contorted or convolute state (Fig. 17b-d). Thus, in the Bonnetioideae the aestivation is intermediate (species of *Bonnetia* and *Neotatea*) or contorted, in the Vismieae it is always quincuncial, and in the Cratoxyleae it is quincuncial (*Eliea*, *Cratoxylum*), intermediate (*Eliea*, *Cratoxylum*, *Triadenum*) or contorted (*Cratoxylum*, *Thornea*, *Triadenum*) (own observations).

In *Santomasia* and *Hypericum*, irrespective of whether the petals are 4, 5 or (abnormally) 6 in number, the aestivation is always contorted. Wydler (1878) describes the direction of twist in *H. elegans* as continuing that of the calyx spiral, and this appears to be the rule in the genus. The number, like that of the sepals, is reduced to 4 in those species of sect. 20. *Myriandra* that have been treated as the genus *Ascyrum* L., as well as in *H. filicaule* (sect. 9. *Hypericum*) and abnormally in some usually 5-merous species. Transitional states

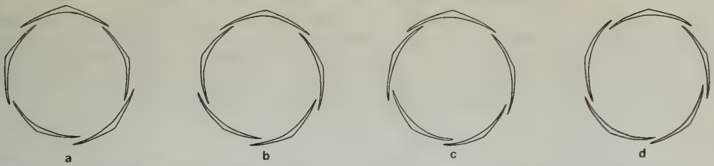

Fig. 17 Corolla aestivation in pentamerous members of the Guttiferae: (a) quincuncial (as in Theaceae); (b, c) intermediate forms (as in *Triadenum fraseri*); (d) contorted (as in *Hypericum*).

can be observed in *H. frondosum* (sect. 20. *Myriandra*) (see p. 198). The numbers of members in these two whorls are almost always the same; only very exceptionally has an extra petal been recorded (e.g. in *H. papuanum*, sect. 26. *Humifusoideum*, and *H. empetrifolium,* sect. 19. *Coridium*).

(*b*) *Form*

A consequence of the constantly contorted aestivation of the petals in *Hypericum* is that, in a given flower, the same margin of each petal is outside in bud. It may be this relationship that has resulted in the development of asymmetry in the petals, a character that is absent in all allied genera except *Santomasia* (and *Cratoxylum*, where it is sometimes slightly developed). This asymmetry is always evident to some extent, except (i) in the smaller, reduced flowers (e.g. of *H. humifusum*, sect. 14. *Oligostema* or *H. japonicum*, sect. 30. *Spachium*) and (ii) in some flowers with a pseudo-tubular corolla (sects 25. *Adenotrias*, 30. *Elodes*). In other, less highly evolved species the inner and outer margins are always distinguishable.

The line of the outer margin is frequently interrupted by a notch or indentation, which results in a more or less evident projection. This marks the limit of the part of the margin that is actually outside in bud and has been termed the *apiculus* (Robson, 1970). Even when an apiculus is not visible, the corresponding point on the margin (which is the morphological apex) is usually recognisable from the pattern of venation and glands. It marks the end of the midrib, which divides the petal into two, usually unequal, parts: (i) an outer, usually thicker and smaller part with denser venation and glands more often laminar, and (ii) an inner, usually larger and thinner part with laxer venation and glands more often marginal.

Hypericum petals are nearly always eligulate, as are those of the Bonnetioideae, most of the other Hypericoideae and all the rest of the Guttiferae. Development of a ligule has occurred in two separate sections of *Hypericum* (25. *Adenotrias,* 28. *Elodes*) and in *Psorospermum, Cratoxylum* (sects *Tridesmos* and *Isopterygium*) and *Eliea* (Perrier de la Bâthie, 1951; Gogelein, 1967; Baas, 1970; Robson, 1974); and in all these taxa except *Cratoxylum* sect. *Isopterygium* and *Psorospermum* (where the appendages are very small), this development is associated with the evolution of a pseudo-tubular flower and specialised insect pollination (Robson, 1972*a*, 1974, 1977*a*). In all but *Hypericum* sect. *Elodes, Psorospermum* and *Cratoxylum* sect. *Isopterygium,* the presence of a ligule is also associated with dimorphic heterostyly; but this association is not essential for the development of heterostyly in the Hypericoideae, as some species of *Vismia* (with petals internally villous) are heterostyled and have no petal ligule (Robson, 1978).

In *Hypericum* sect. 25. *Adenotrias* the ligule is entire, concave and cucullate; and it is pressed closely against the ovary, thus leaving a gap opposite each sepal. In sect. 28. *Elodes*, however, it is flat and trifid, and the association with the ovary is less close. In both sections the ligule is long, non-vascular and united with the petal lamina for most of its length.

These appendages have been termed nectary scales, but they do not appear to secrete nectar. Their function may be purely structural (associated with the pseudo-tubular corolla), or there may be juicy cells between them and the petal lamina which are pierced by insect tongues. This question has not yet been investigated anatomically. What seems clear, however, is that they have the same morphological status as petal ligules in, for example, the Ranunculaceae or Amaryllidaceae. It remains to be discovered whether the ligules in the other Hypericoid genera are non-vascular like those of *Hypericum*. At any rate, the primitive petal in the subfamily (as in the Bonnetioideae) would appear to be eligulate.

(*c*) *Colour*

In the Guttiferae sensu lato the petal colour varies from white and yellow or green to shades of red; blue is entirely absent. Almost the whole of this range of colour is represented in the Hypericoideae, but the tribes of this subfamily are more limited in this regard. The Vismieae have shades of white, yellow and green; in the Cratoxyleae yellow is replaced by red, the petals being white or pink to red, sometimes tinged with green; whilst in the Hypericeae green is absent and the basic petal colour is normally a shade of yellow, often with red tinges or markings. Rarely in *Hypericum* is the basic colour white, and then the tinges and markings are pink. This effect appears to be due to the red anthocyanin's becoming paler when the basic flavonoid is white instead of yellow.

The yellow basic (flavonoid) colour in *Hypericum* varies from orange (aurantiacus), e.g. in *H. bequaertii* and several species in sect. 30. *Spachium*, through dark yellow (luteus) and golden yellow (aureus) to pale yellow (flavus). Occasionally an even paler shade (citrinus) occurs as a 'sport', e.g. in *H. olympicum* forma *minus* Hausskn. c.v. Sulphureum (sect. 10. *Olympia*) (Robson, 1980*b*) and *H. hirsutum* var. *pallidum* Rouy & Foucaud (sect. 18. *Taeniocarpium*) (Druce, 1923; Brenan, 1945). Pure white forms are very rare but have been recorded in *H. geminiflorum* (sect. 4. *Takasagoya*), from Luzon (Merrill, 1909 : 294, as *H. loheri*) and probably Taiwan (Robson, 1976), and *H. aviculariifolium* (sect. 12. *Origanifolia*) (Robson, 1967*a*, *b*). This colour variation is rarely of taxonomic significance above the species level, but certain generalisations can be made. Thus, the deeper shades (apricot, orange) occur only in sects 1. *Campylosporus*, 29. *Brathys* and 30. *Spachium*; deep yellow is more widespread (e.g. in *Santomasia* and *H. acmosepalum*, sect. 3. *Ascyreia*) but is not confined to a particular section; in sect. 9. *Hypericum* the petals tend to be golden yellow, whereas in sect. 27. *Adenosepalum* they are usually paler in colour.

The red colour (anthocyanin) usually occurs in the outer dorsal part of the petal, either confined to the veins (e.g. in *H. trichocaulon*, sect. 13. *Drosocarpium*) or as a more or less extensive tinge. In only one taxon has it extended over the whole corolla (and calyx), resulting in a 'red-flowered *Hypericum*' (*H. capitatum* var. *capitatum*, sect. 17. *Hirtella*); but other members of the same species (*H. capitatum* var. *luteum* N. Robson) have no red colour in these organs (Robson, 1967*a*, *b*). Again, whereas *H. tetrapterum*, like most of sect. 9. *Hypericum*, has no petal anthocyanin, its sister-species *H. undulatum* frequently has red-tinged petals. They are wholly yellow only in var. *boeticum* (Boiss.) Lange, which is intermediate in form and distribution between the type variety and *H. tetrapterum*.

The presence of anthocyanin in other parts of the *Hypericum* plant is often an indication of an unfavourable environment; and this association may be relevant with regard to *H. capitatum*, which grows in a habitat that approaches desert more nearly than does that of any other *Hypericum*. But the function of the red tinges has been shown to be related to insect visitation (see p. 122).

(*d*) *Venation*

In common with the rest of the Guttiferae and the other families in the Dilleniidae, *Hypericum* and *Santomasia* have 1-trace petals (Saunders, 1937; Robson, 1956, 1972*a*) (Fig. 32, p. 129). In larger petals (e.g. those of *H. forrestii*, sect. 3. *Ascyreia*) the subsequent basal dichotomies form a slender midrib and two thicker traces which, in turn, very soon dichotomise repeatedly to form a series of veins of roughly equal width (Robson, 1972*a* : fig. 3) (Fig. 18b). In smaller petals the branchings are fewer, and the small petals of some herbs in

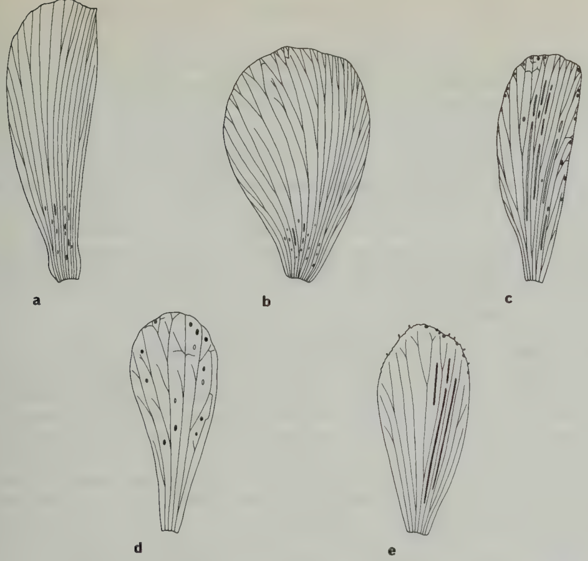

Fig. 18 Variation in venation and glandularity of petals in *Hypericum* (numbers indicate sections); (a) *H. styphelioides* (29); (b) *H. forrestii* (3); (c) *H. perforatum* (9); (d) *H. asperulum* (17); (e) *H. elodeoides* (27) (a, b x 2·5; c x 3·5; d x 4; e x 5).

sect. 30. *Spachium* have only three, unbranched veins. The veins are crowded and little-branched in the morphologically outer part of the petal but more widely spaced and more frequently dichotomising in the inner part (Fig. 18a).* Towards the margin they sometimes form loops or lambda junctions (Melville, 1969, 1976) with adjacent veins (Fig. 18b–d); but they frequently reach the margin unbranched (Fig. 18b) or (sometimes excepting the midrib) stop short of it without forming a loop or junction (Fig. 18e). The evolutionary progressions in general seem to be:

Veins numerous → few; much-branched → unbranched; free → looped or joined; all reaching margin → only midrib reaching margin → none reaching margin.

(*e*) *Glandularity*

The petal glands in *Hypericum* are comparable with those of the sepals, except that truly inframarginal glands are rare. When the glands form a distinct peripheral row, they are dark and usually touch or interrupt the margin in some way. Such a row is present in the petals of *Santomasia* in the form of glandular cilia or sessile glands, sometimes along with a few larger submarginal dark glands (Fig. 1e). In all other genera of the Hypericoideae, as well as those of the Bonnetioideae, the petal margin is always entire and marginal glands are absent. Their presence in the Hypericeae may therefore be regarded as an advance. Once acquired, however, they can be lost again (e.g. in sect. 3. *Ascyreia*) and then reacquired (e.g. in

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*In *Archytaea* (Bonnetioideae), on the other hand, the petal is symmetrical and the veins are equal and symmetrical also, cf. Maguire (1972 : fig. 2d).

sect. 9. *Hypericum*); and so their presence is taxonomically significant at the sectional level at most.

(i) Laminar glands. In *Santomasia* and primitively in *Hypericum* the crowded veins towards the base of the petal alternate with pale glandular lines, which are always interrupted distally to some extent; but in the thick petals of these taxa, the lines may be easily visible only towards the base, and then incompletely as a series of dots (Figs 1e, 18a, b). The inner, thinner part always remains eglandular (Fig. 18c). The interruptions become gradually more numerous to form streaks and eventually dots (e.g. in sects 17, 18 and 19) (Fig. 18d). They are sometimes much reduced in number as well as size; but they never disappear entirely in a section where they are present in the primitive members. They do, however, seem to be absent entirely from sects 25. *Adenotrias* and 30. *Spachium.*

In addition to this variation in form and distribution, the petal laminar glands may become dark or reddish. The whole gland may be dark (e.g. in *H. elodeoides*, sect. 27. *Adenosepalum* (Fig. 18c), or only parts of a glandular line may be dark and the rest pale (e.g. in *H. oliganthum*, sect. 9. *Hypericum*).

(ii) Marginal glands. The presence of truly marginal petal glands in the Bonnetioideae–Hypericoideae affinity is confined to the Hypericeae, and it is probably a derived character in this tribe. In *Hypericum* it has become constant in the less primitive members of sect. 1. *Campylosporus*, in two groups derived from sect. 3. *Ascyreia* (the *Olympia* group, i.e. sects 10–16, and sect. 17. *Hirtella*), and in some members of sects 9. *Hypericum*, 18. *Taeniocarpium* and 27. *Adenosepalum*. It therefore appears that the occurrence of marginal petal glands in *Hypericum* is polyphyletic, and it possibly indicates a certain minimum concentration of hypericin in the petals (see p. 149). Their presence in *Santomasia* and sect. 1. *Campylosporus*, respectively, is to be regarded as a local specialisation, a trend that is reversed in sects 27. *Adenosepalum* and 28. *Elodes*. Here the gradual diminution in the concentration of hypericin is reflected in the petal marginal glands, which are present in the primitive (Macaronesian) species but absent from the most advanced ones.

The marginal glands may be sessile (e.g. in *H. revolutum* subsp. *keniense*, sect. 1. *Campylosporus*) or on cilia (e.g. sometimes in *H. revolutum* subsp. *revolutum*). Where they occur in the *Hirtella* group (sects 17–19) they are usually on cilia, whereas they are nearly always sessile (and often in a marginal depression) in the *Olympia* group (sects 10–16) and sect. 9. *Hypericum*, except in *H. sampsonii* (sect. 9. *Hypericum*), where they are on cilia. Where they do occur they are nearly always confined to, or are more strongly developed on, the inner margin; and they are always dark except in *H. orientale* (sect. 16. *Crossophyllum*) and some advanced members of sect. 27. *Adenosepalum*, where they are reddish or amber. In both these groups, as has already been mentioned, there would seem to have been a diminution in the concentration of hypericin.

(f) Corolla shape

In general, *Hypericum* corollas are radiate, i.e. the petals spread out or become reflexed. The only notable exceptions are: (i) where the sepals remain erect and confine the petals, forming a pseudo-tubular subrotate corolla (sects 25. *Adenotrias*, 28. *Elodes*) and (ii) in *H. bequaertii*, where the petals remain erect so that the corolla is campanulate. It is not clear whether this form is primitive in *Hypericum* or derived. On the one hand, erect petals occur in *Santomasia* and in primitive genera of the Moronobeoideae (*Pentadesma* Sabine and *Montrouziera* Planchon & Triana), as well as in the Vismieae and Cratoxyleae. On the other hand, radiate corollas are almost universal in the rest of the Guttiferae (including the Bonnetioideae). As *H. bequaertii* seems to have differentiated from the *H. revolutum* subsp. *keniense* (with a radiate corolla) in response to peculiar climatic conditions of the high Ruwenzori (Robson, 1979), perhaps the campanulate corolla is best regarded as a local specialisation.

(*g*) *Corolla movement*

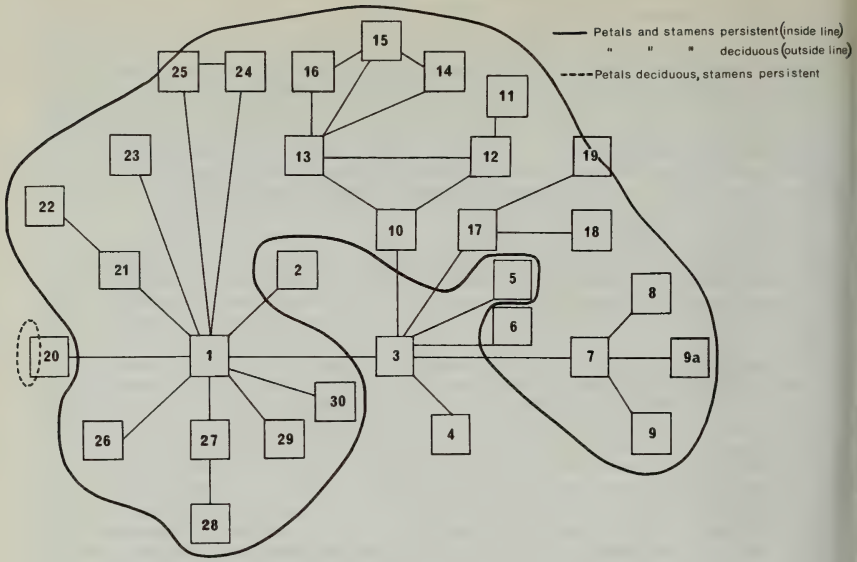
With the above-mentioned exceptions, the petals in *Hypericum* spread more or less widely or become reflexed. This movement may occur once (e.g. in sect. 3. *Ascyreia*) or may be repeated daily for a few days (e.g. in sect. 10. *Olympia*). In some species of sect. *Ascyreia*, however, the concave petals do not become reflexed but form a shallowly cupuliform corolla (compare the reflexed petals of *H. kouytchense* with the ascending ones of *H. beanii* in Robson, 1970 : figs 235, 240). The extremely reflective surface of the petals in this section would produce the effect of a paraboloid mirror in a cupuliform corolla and might concentrate the sun's rays to some extent, raising the temperature inside the flower.

(*h*) *Corolla (and androecium) persistence*

One of the features used by Keller (1893, 1925) in classifying *Hypericum* was whether or not the petals and stamens were deciduous immediately after anthesis, and this has proved to be a useful character at sectional level (Robson, 1977*a* : fig. 1). In general the petals and stamens behave similarly in this regard, which is not surprising when one considers that petal and stamen fascicle together form an androphyll (Melville, 1963) and are supplied by the same vascular trunk (Robson, 1956, 1972*a*). The only exception to this rule is found in all but two species of sect. 20. *Myriandra* subsect. *Pseudobrathydium*, in which the stamens remain when the petals fall (Adams, 1962*a*) (Fig. 5). It may be significant that this change in behaviour has occurred in the one section where, the individuality of the fascicles having been completely lost, the stamens in the primitive species are shed individually, not as fascicles.

A similar development seems to have occurred in the Bonnetioideae. In *Ploiarium*, where the androecium is obviously fasciculate, both petals and stamens are deciduous; whereas in the other genera, where the androecium is outwardly afasciculate, the stamens are persistent and the petals deciduous. It is not yet clear whether deciduous or persistent petals are primitive in the Guttiferae as a whole. From first principles, deciduous ones would be derived; but, as we have seen, the change seems to be easily reversible and would not therefore appear to be fundamental. In *Hypericum* this is certainly so (Fig. 19). In sect. 1. *Campylosporus* both petals and stamens are persistent; but they have become deciduous in three adjacent sections or groups, viz. sect. 2. *Psorophytum*, sects 3–5 (*H. socotranum* is transitional) and sect. 20. *Myriandra* (*H. quartinianum* and *H. synstylum* are transitional). In two further sections, 19. *Coridium* and 25. *Adenotrias*, the change has been intrasectional. Reversion to persistent stamens has taken place in sect. 20. *Myriandra*; and persistent petals and stamens are constant in all the sections derived from 3. *Ascyreia* (i.e. sects 4–19) with the exception of 4. *Takasagoya*, 5. *Androsaemum* and the above-mentioned part of 19. *Coridium*.

The biological significance of deciduous floral members in *Hypericum* is not clear. Where all outer members fall, as in *H. hircinum* (sect. 5. *Androsaemum*) or the primitive members of sect. 20. *Myriandra*, the fruit is naked. Where the sepals remain, as in sect. 3. *Ascyreia*, they have no obvious function (e.g. of protection). Where all whorls remain for at least some time after the corolla and androecium have withered, the inner ones may behave in two distinct ways. In *H. olympicum* and most species of the *Olympia* and *Hirtella* groups (sects 10–19) they twist up round the developing fruit, forming a bud-like protective covering. In other species (e.g. sect. 7. *Roscyna* and most of sect. 9. *Hypericum*) the withered petals remain spreading or reflexed and twist or curl, and the stamens become suberect. Although the behaviour of the corolla is characteristic of whole groups of species, it must be used taxonomically with care. For example, although in most of the *Olympia* group the withered whorls become bud-like, in some species of sect. 13. *Drosocarpium* (e.g. *H. perfoliatum*) they remain spreading. In contrast, although in many species of sect. 9. *Hypericum* they remain spreading, in *H. undulatum* they become bud-like. There may be a correlation between the relative width of the petals and their behaviour; I can think of no other explanation of this phenomenon.


—— Petals and stamens persistent (inside line)
" " " deciduous (outside line)
----Petals deciduous, stamens persistent
15
25
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9a
30
4
26
27
29
9
28

Fig. 19 Distribution of deciduous petals and stamens in *Hypericum*.

Stamens

(*a*) *Number and arrangement*

The association between petals and stamen fascicles mentioned above suggests that the fascicle of stamens, rather than the individual filament + anther, is the androecial unit in *Hypericum*, and the correlation of five free antipetalous fascicles with other primitive characters in sects 1–4 makes this hypothesis more likely. In contrast, to suggest that fascicles have resulted from 'dédoublement' or 'secondary polyandry' (Moquin-Tandon, 1826; Payer, 1857; Saunders, 1936; Leins, 1964, 1971) or from aggregation of stamens or sectorial sterilisation in a polyandrous flower (Goebel, 1898–1901; Hirmer, 1917; Corner, 1946) makes nonsense of other trends in the genus (Robson, 1956, 1972*a*). The only species which sometimes have five single antipetalous stamens (*H. gentianoides* and *H. aphyllum* Lundell, sect. 30. *Spachium*) are annual herbs with leaves reduced to scales; and the apparently polyandrous species (in sects 20. *Myriandra*, 29. *Brathys* and 30. *Spachium*) are all specialised in several respects in comparison with those of sect. 1. *Campylosporus*. The stamen fascicle in *Hypericum* thus appears to be a reduced branching system such as is envisaged in the Telome Theory (Zimmermann, 1959; Wilson, 1937, 1953) and Gonophyll Theory (Melville, 1963).

If the stamen fascicles form the antipetalous androecial whorl then the antisepalous whorl is normally absent in *Hypericum*. In *Santomasia*, however, as we have already seen, the latter is present as small sterile projections between the stamen fascicles (Fig. 1g). Comparison with related taxa shows that the diplostemonous pentamerous androecium with each member represented by a multistaminate (usually fasciculate) structure should be regarded as primitive in the Dilleniidae (cf. Wilson, 1965, 1973; Stebbins & Hoogland, 1976). In some orders (e.g. Malvales, Violales) it is the antipetalous whorl that is reduced or absent (van Heel, 1966); in others it is the antisepalous one (e.g. Theales, Myrtales*), whilst in still others (e.g. Ericales) both are equally reduced—to one-stamened members. A transitional state to the Malvalean one is found in *Saurauia* (Saurauiaceae), where Brown (1935) showed that the apparently polyandrous androecium develops as five single antipetalous stamens and five groups of antisepalous ones. In the Guttiferae sensu lato both whorls are sometimes present, but the only genus in which they are both known to be fertile is *Decaphalangium* Melchior (1930) from Amazonian Peru. It seems likely, however, that anatomical investigation will show that both whorls are present in at least some species of *Clusia* and its relatives. In other tribes the antipetalous whorl is sterile or absent (Table 3).

(*b*) *Modifications of fascicles*

If the fascicle is a reduced branching system, then this reduction has resulted in the virtual elimination of the primitive fascicle trunk above toral level. There would appear to be no extant species of the Dilleniales–Theales evolutionary line in which the stamen fascicle has a

Table 3 Characters of the androecium in bisexual and male flowers of the Guttiferae

Taxon	Antisepalous whorl		Antipetalous whorl*	
	Presence and fertility†	No. and union of fascicles	No. and union of fascicles	Union of filaments
Bonnetioideae	s or a	5	5 or (5)	free
Hypericoideae				
Hypericeae	s or a	5 (*Santomasia*), 0, 3 (*Hypericum* sects 25, 28)	5, (5), (4), (2) + 1 + 1 + 1, (2) + (2) + 1	free or partly united (*Hypericum* sects 25, 28, 30 pp.)
Vismieae	s	5	5	partly united
Cratoxyleae	s	3	(2) + (2) + 1	partly united
Moronobeoideae	s	5, (5)	5, (5)	free to wholly united
Calophylloideae	a	0	(5), (4)	free to wholly united
Clusioideae				
Clusieae	f (? or a)	5, (5) (? or 0)	5 (5)	free to wholly united
Decaphalangium	f	5	5	wholly united
Allanblackia	s	5	5	wholly united
Garcinieae	s or a	5, (5), 4, (4)	5, (5), 4, (4), 3	free to wholly united

*The antipetalous whorl is always fertile, except in ♀ flowers of dioecious species.
†s = sterile, f = fertile, a = absent.

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*The placing of part of the Myrtales in the Rosiidae by Cronquist (1968) on the basis of the direction of stamen development may be found to be erroneous when other characters have been taken into consideration. Whether the androecium develops centripetally or centrifugally is a less fundamental character than Cronquist supposed (cf. Leins, 1964; Sattler, 1976; Tucker, 1976).

single vascular trace branching well above the torus. All 'branching stamens' that have been studied have proved to have separate staminal traces running from the region below toral level where the trunk trace dichotomises, e.g. *Hibbertia* (Dilleniaceae) (Wilson, 1965), *Garcinia* (Stebbins, 1974 : fig. 12–1), and *Vismia* and *Cratoxylum* (Robson, 1956, 1972*a*). These stamen fascicle trunks are therefore the result of secondary fusion of filaments, as they are in *Hypericum* sects 25. *Adenotrias*, 28. *Elodes* and part of 30. *Spachium*. The tissue of the primary trunk remains at the base of some fascicles (e.g. in species of *Camellia* or *Hypericum* with distinct fascicles), but any higher fusion should be attributed to this secondary union. Thus, within-fascicle modifications have resulted in either (i) the complete elimination of the fascicle trunk and the merging of the constituent stamens to form a 'polyandrous' androecium (e.g. in *Hypericum* sect. 20. *Myriandra* and most genera of the Bonnetioideae and Myrtaceae) or (ii) the secondary fusion of the filaments and sometimes the anthers to form a markedly fasciculate androecium (e.g. in some species of *Hibbertia* sect. *Candollea* (Wilson, 1965), *Garcinia* and the Moronobeoideae) or (iii) reduction of the fascicle to a single stamen (e.g. in *Hypericum gentianoides*, sect. 30. *Spachium*).

As well as within-fascicle modification there is between-fascicle modification, in that the fascicles themselves may unite, either altogether to form a tube (as in *Endodesmia*, Calophylloideae, or *Symphonia*, Moronobeoideae) or in pairs 2 + 1 + 1 + 1 or 2 + 2 + 1 (as in the Cratoxyleae and various sections of *Hypericum*). The latter modification has also occurred in the *Cucurbitaceae* (Violales), but after reduction of the fascicle to one stamen (Chakravarty, 1955).

A summary of androecial variation in the Guttiferae is given in Table 3 (modified from Robson, 1972*a*).

(*c*) *Androecial trends*

The reasons for regarding the afasciculate androecium in *Hypericum* as derived were discussed in Part I (Robson, 1977 : 303). It remains to outline the androecial trends in the genus as a whole (Fig. 20).

The primitive condition of five free antipetalous fascicles (Fig. 20a) occurs constantly in the first seven sections except 2. *Psorophytum*, in which *H. balearicum* frequently has four fascicles due to the coalescence of the pair on either side of sepal 5 (Fig. 20b). The spatial and developmental reasons for this fusion are the same as those pertaining to the variation in sepal size and arrangement (p. 86) (see Hirmer, 1917; Breindl, 1934 : esp. fig. 33). The four-fascicled state seems to be relatively unstable, as it usually occurs only as an abnormality or a transitional evolutionary stage to the three-fascicled state (Fig. 20c). This is widespread in the genus and results from the additional coalescence of the pair of fascicles on either side of sepal 4. The double fascicles have more stamens than the single one (unless numbers are very small), the one on the radius of sepal 4 being larger than that on radius 5 (Saunders, 1936). The three fascicles thus formed usually remain distinct and the configuration stable; but in two sections there has been a reversion from long-established trimery to pentamery, viz. sects 13. *Drosocarpium* (the Cyprus population of *H. repens* = *H. modestum* Boiss.) and 15. *Thasia* (*H. thasium*); and in sects 11. *Campylopus* (*H. cerastoides*) and 26. *Humifusoideum* the number of androecial members is less stable. In *H. cerastoides* it varies from five to three, and the fascicles are frequently difficult to recognise owing to their uniting to form a very shallow ring (Fig. 20c, e–g). In 26. *Humifusoideum*, however, there is no ring-formation, and the individuality of the fascicles is lost merely by merging (Fig. 20f, g). As this alteration is less fundamental than the one to a distinct 2 + 2 + 1 formation, it can be more easily reversed to a rather indefinite pentamery, a change that parallels a reversion from trimery to pentamery in the gynoecium: *H. papuanum* 3 (4–5), *H. natalense* 3–4–5, *H. wilmsii* 3–4, *H. peplidifolium* (4)5 (cf. Saunders, 1937; Robson, 1956, 1958*b*, 1973*a*; Killick & Robson, 1976).

A similar slight merging of the fascicles in sect. 30. *Spachium* has resulted in changes comparable with those in sect. *Humifusoideum* but more far-reaching. In the more primitive

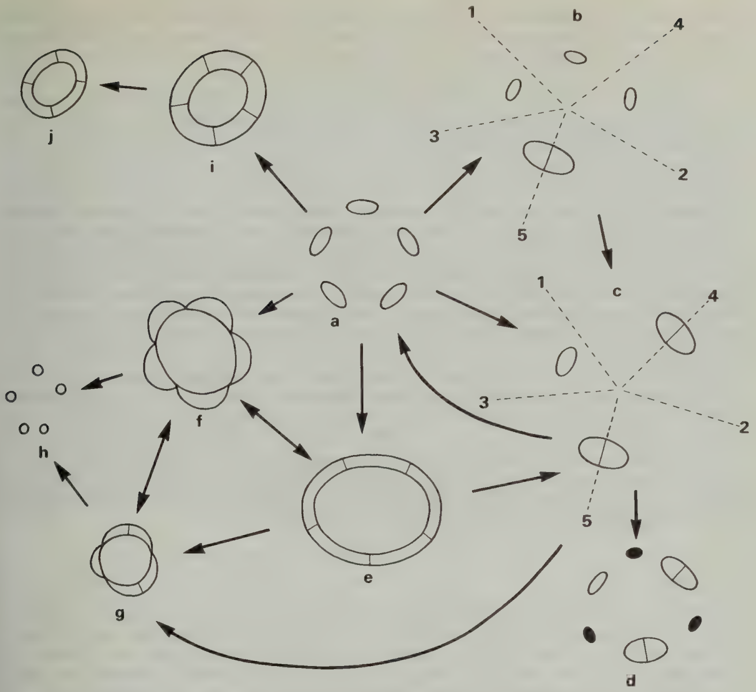

Fig. 20 Androecial configuration trends in *Hypericum*: (a) 5 free fascicles; (b) 2 + 1 + 1 + 1 fascicles, i.e. condensation along radius S5; (c) 2 + 2 + 1 fascicles, i.e. condensation along radii S5 and S4; (d) reappearance of 3 alternipetalous fasciclodes (sterile fascicles); (e) union of fascicles to form a narrow continuous ring; (f) merging of fascicles with partial obscuring of members ('5 obscure fascicles'); (g) merging of fascicles along with radial condensation ('3 obscure fascicles'); (h) reduction of each fascicle to a single stamen; (i) union of fascicles with radial condensation to form a broad continuous ring; (j) elimination of one androecial member, resulting in tetramery.

species, e.g. *H. brasiliense*, five distinct fascicles can sometimes be observed (Fig. 20a, f), and in two species that are rather isolated taxonomically (*H. piriai*, *H. hilaireanum*) there are three fascicles with the filaments in each one united for half their length or more (Fig. 20c). In most of the section, however, the stamens form a ring, initially continuous (Fig. 20e) but gradually becoming more irregular in the more advanced, smaller-flowered species (Fig. 20f, g). Eventually, in this evolutionary trend, the reduction in stamen number results in the reappearance of five fascicles (e.g. in *H. oligandrum* and *H. pleiostylum*); and these are ultimately each reduced to a single stamen in *H. gentianoides*, the type species of *Sarothra* L., which was placed by Linnaeus (1753) in his Pentandria Trigynia (Fig. 20h). In both sects 20. *Myriandra* and 29. *Brathys*, on the other hand, the ring of stamens remains continuous. As will become evident later (p. 138), these sections show differing trends toward reduction in the size of the torus. In *Brathys* the condensation is mainly vertical and results in a relatively broad torus with a narrow ring of free stamens, and the perianth and androecium remain constantly pentamerous (Fig. 20e). In *Myriandra*, however, the condensation is primarily lateral and produces a relatively narrow torus with a broad ring of free stamens (Fig. 20i). There is therefore more radial congestion on the torus, so that tetramery becomes established in the three outer floral whorls (Fig. 20j).

The reappearance in sects 25. *Adenotrias* and 28. *Elodes* of three sterile members of the outer whorl in connection with the evolution of specialised insect pollination (Fig. 20d) has been discussed already (Robson, 1972*a*) and will be mentioned again later (p. 123).

(*d*) *Form and glandularity*

The stamens of *Hypericum* and *Santomasia*, like those of most of the Bonnetioideae (Maguire, 1972) and of some of the rest of the Guttiferae (Calophylloideae, Vismieae, Cratoxyleae), have small, almost isodiametric tetrathecal anthers, which dehisce introrsely by longitudinal slits, and slender filaments. The stoutest filaments are found in *H. bequaertii*, but neither they nor the anthers vary in form in a taxonomically useful way. Unlike the essentially basifixed anthers of the Bonnetioideae, those of *Hypericum* are dorsifixed, the apparently basifixed ones in sect. 4. *Takasagoya* resulting from heterogonic growth (Robson, 1973*a*).

Terminating the connective is a flat or hemispherical gland which varies in colour from amber to red or black according to the amount of hypericin that it contains. Thus it is amber in sects 3. *Ascyreia*, 20. *Myriandra* and 30. *Spachium*, for example, and black in several sections including 9. *Hypericum* and 27. *Adenosepalum*. Comparable connective glands occur in some genera of the Bonnetioideae (Maguire, 1972 : fig. 20), where they are cupuliform, and in the rest of the Hypericoideae, where they are sometimes paired (e.g. in *Cratoxylum*). In *Neotatea neblinae* (Bonnetioideae), Maguire (1972 : fig. 26) depicts what appears to be a glandular exudate at the apex of the anther.

(*e*) *Colour*

The stamens in *Hypericum* are nearly always the same colour as the petals, the exceptions being *H. calycinum* and its hybrid with *H. patulum* (*H.* x *moseranum* André) (sect. 3. *Ascyreia*) and *H. pulchrum* (sect. 18. *Taeniocarpium*), where the anthers are crimson. The orange colour in the anthers of *H.* x 'Hidcote', contrasting with the golden petals, is no doubt due to the influence of one of its parents, probably *H. calycinum* (see p. 170).

(*f*) *Length and movement*

The stamens are almost always shorter than the petals, exceeding them only in *H. hircinum* (sect. 5. *Androsaemum*), and their relative length is often a useful specific character. They vary in length within a fascicle, and so measurements in the specific descriptions will always refer to the longest stamen.

The longer stamens are always on the outside of the fascicle or ring and are therefore the first to spread at anthesis. Later, when the stamens close up again, these longer ones may become entangled with the styles and effect self-pollination.

(*g*) *Staminodial members*

The occurrence (in *Santomasia* and other Hypericoid genera) or reappearance (in *Hypericum* sects 25 and 28) of conical or ligulate bodies between the stamen fascicles has been discussed above and in earlier works (Hochreutiner, 1918; Robson, 1972*a*, 1977*a*). Morphologically they are sterile antipetalous stamen fascicles, not stamens, and so the term 'staminode' seems to describe them inappropriately. In previous publications (e.g. Robson, 1967*b*, 1972*a*) I have used the word 'fasciclode' (i.e. a sterile fascicle), which describes the nature of the organ more accurately, if somewhat inelegantly. In *Hypericum* and some other genera they act as lodicules, expanding to spread the petals; but this word cannot be applied generally, and so 'fasciclode' is the better term to use, especially if the first 'c' is not pronounced.

Ovary

(*a*) *Gynoecial elements*

The gynoecium in *Hypericum*, as in the rest of the Guttiferae, is superior and occupies the whole central part of the torus, i.e. there is no evidence of a disk, a perigynous zone or a gynophore. Like the members of the Bonnetioideae, Calophylloideae (except *Mammea*) and the other Hypericoideae, *Hypericum* has an ovary surmounted by elongate styles, each of which is terminated by a stigmatic surface. These styles vary in number from 5 to 2, as do the placentae, ovary lobes and capsule valves. They may be completely free or more or less coherent or united; but the stigmas remain distinct, or at least identifiable by the number of lobes, except in sect. 4. *Takasagoya*. There is therefore never any difficulty in determining the number of gynoecial elements (carpels, gynophylls, etc.) that are present in *Hypericum*. The variations in these gynoecial characters in the Guttiferae are shown in Table 4. The gynoecium of the Myrtaceae resembles that of the Hypericoideae and Bonnetioideae in length of styles and in placentation, differing essentially only in having an inferior ovary.

The gynoecial elements will be termed 'carpels' in discussion for convenience, but without any implication of acceptance of the Candollean theory of the carpel. Indeed, gynoecial and fruit structure in *Hypericum* lends support rather to the Gonophyll Theory (Melville, 1962).

Table 4 External characters of the gynoecium in the Guttiferae

Taxon	No. of elements	Style length*	Style and stigma union†
Bonnetioideae	5, 3	l	f, u
Hypericoideae			
Hypericeae	5–2	l	f, u
Vismieae	5	l	f
Cratoxyleae	(5–4) 3	l	f
Calophylloideae			
Paramammea	4	l	f, u
most genera	(4) 2–1	l	u
Mammea	(4) 2	s	u
Poeciloneuron	2	l	f
Moronobeoideae	5	l	u
Clusioideae			
Clusieae	(4) 5–6 (10)	s, a	f
Decaphalangium	5	s[x]	f[x]
Allanblackia	5	s	u
Garcinieae	(3) 4–5 (–12)	s, a	u

*l = long (i.e. noticeably extended), s = short (not quite absent), a = absent
†f = free, u = united (when styles are absent this applies to stigmas)
[x] only male flowers described

(*b*) *Relationships with other whorls*

When one considers the exigencies of space on a developing floral receptacle, it is not surprising that a trend towards oligomery in *Hypericum* (Fig. 6) effects the innermost (gynoecial) floral whorl first. For example, in sect. 5. *Androsaemum* the outer whorls are 5-merous and the gynoecium 3-merous. The statement by Keller (1925) that *H. peplidifolium* (sect. 26. *Humifusoideum*) has 3 stamen fascicles and 5 styles, thus providing an exception to this rule, was shown to be due to faulty observation (Saunders, 1937; Robson, 1956).

This meiomeric tendency is associated with the crowding along the radii of sepals 4 and 5 noticed by Breindl (1934) and Saunders (1936), which was discussed in connection with the quincuncial development of the calyx (p. 86). Although there should theoretically be somewhat greater crowding along radius 5 than along radius 4, the difference is slight. This explains why there is usually an evolutionary 'jump' from 5-mery to 3-mery, the intermediate 4-mery being an unstable state and never solely characteristic of a species (Fig. 21). Where it does occur (e.g. in sects 2. *Psorophytum*, 9. *Hypericum* and 26. *Humifusoideum*), it is associated with a 4-fascicled or irregular androecium (Fig. 6). The biological advantage of this arrangement, whereby the styles continue to alternate with the stamen fascicles or groups, should be noted. The extension of this meiomerous trend to 2-mery has occurred rarely in *Hypericum*, where it is associated with either 4-mery of the outer whorls (in sect. 20. *Myriandra*) or extreme reduction in flower size (in sect. 30. *Spachium*).

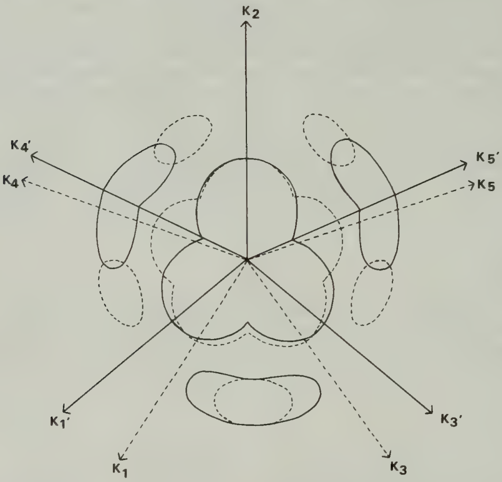

Fig. 21 Transition from 5-mery (dotted lines) to 3-mery (solid lines) in the inner floral whorls of *Hypericum* (after Breindl, 1934). The crowding along sepal radii 4 and 5 is accompanied by a corresponding widening of the angle between sepals 1 and 3. Note that the theoretically equal angles are never found in practice, owing to the transition from opposite to quincuncial phyllotaxis (see p. 86).

At this point it is perhaps desirable to warn against explaining these spatial relationships in causal terms. As Goebel (1898–1901 : 712, footnote) said [my translation]: 'If we can see in a flower that more numerous primordia appear where there is more room at the floral apex, this does not necessarily mean that we can say that space relationships are responsible for the numerical relationships; we can just as well assume that there is more space provided where the floral apex is most disposed to form organ primordia. All 'mechanical' explanations are excluded in these relationships.'

On the other hand, Goebel's own suggestion that nutritional differences may be involved is equally unconvincing. The expression of a genotype can be very much modified by variations in nutrition; but one cannot validly attribute differences between plants with *different* genotypes to such variations alone, although the genotypes probably influence the nutritional requirements of the respective plants.

(*c*) *Shape and proportions*

The ovary in *Hypericum* varies in absolute size and in shape from narrowly elliptic or narrowly ovoid to globose, but these variations are of only minor taxonomic value. Of greater value are the relative proportions of styles and ovary, which vary quite widely. In *H. bequaertii* and *H. revolutum* (sect. 1. *Campylosporus*), the styles are about 1·2–1·6 times as long as the ovary, whereas in *H. monogynum* (sect. 3. *Ascyreia*) they are 3·5–5 times as long as the ovary. This change in proportion is due more to a reduction in ovary length by half than to an increase in style length, although that, too, has occurred. In *H. olympicum* (sect. 10. *Olympia*) the relative style length (4–5 times) may be seen to be due almost entirely to a decrease in ovary size when compared with related species in sect. 3. *Ascyreia*. On the other hand, the styles of *H. japonicum* (sect. 30. *Spachium*), which are only 0·2–0·3 times as long as the ovary, appear to have attained their present proportions largely as a result of an absolute decrease in style length.

(*d*) *Union of styles*

The styles in the primitive Hypericeae are erect and appressed, but free (as in *Santomasia*) or only slightly coherent (as in *Hypericum bequaertii*), eventually turning outward near the apex. This state is comparable with that of primitive members of the Moronobeoideae (*Pentadesma*) and Calophylloideae (*Mesua*), where the union of the styles is more intimate, and with that of the Bonnetioideae, where the 5 styles of *Ploiarium* are free and outcurved but the 3–5 styles of the other genera are completely united.

Within *Hypericum* there has been a trend towards fusion of the styles in two parts of the genus. In sect. 1. *Campylosporus*, complete union is achieved in *H. synstylum*, *H. quartinianum* and *H. roeperanum*; but the union is relatively loose, as the sections derived from this part of sect. 1 have styles that either are completely free and divergent from the base (sects 21. *Webbia*, 22. *Arthrophyllum*, 27. *Adenosepalum*, 28. *Elodes*) or separate as the fruit matures (sect. 20. *Myriandra*). In the other trend the fusion becomes more intimate, as the styles do not separate in fruit in *H. monogynum*, *H. prattii* or *H. longistylum* (sect. 3. *Ascyreia*), whilst in sect. 4. *Takasagoya* (which is derived from this group of species) the fusion is complete, even the stigmas having lost their individuality. From the same part of sect. 3 is derived sect. 7. *Roscyna*, in whch the fusion trend is reversed, even within one widespread variable species (*H. ascyron*), with the result that in the derivative sections 8. *Bupleuroides*, 9. *Hypericum* and 9a. *Concinna* (see p. 173) the styles are free and (in the last two) become gradually more divergent (Fig. 22).

(*e*) *Stigmas*

The stigmas in *Hypericum bequaertii* are subglobose, i.e. they are wider than the style. Modifications, which are often of taxonomic value, have led to extreme reduction in width (e.g. in sect. 20. *Myriandra*, where the stigma is narrower than the upper part of the style) or to elaboration in the form of capitate stigmas, which are characteristic of certain parts of sects 29. *Brathys* and 30. *Spachium*. In some species of these sections the broadening of the stigma is correlated with a gradual upward broadening of the style.

(*f*) *Glandularity*

The ovary walls of *Hypericum* include resin-containing canals or glands. Although they are often visible in the flower, they tend to enlarge and become prominent in fruit and will therefore be discussed under that heading (p. 109).

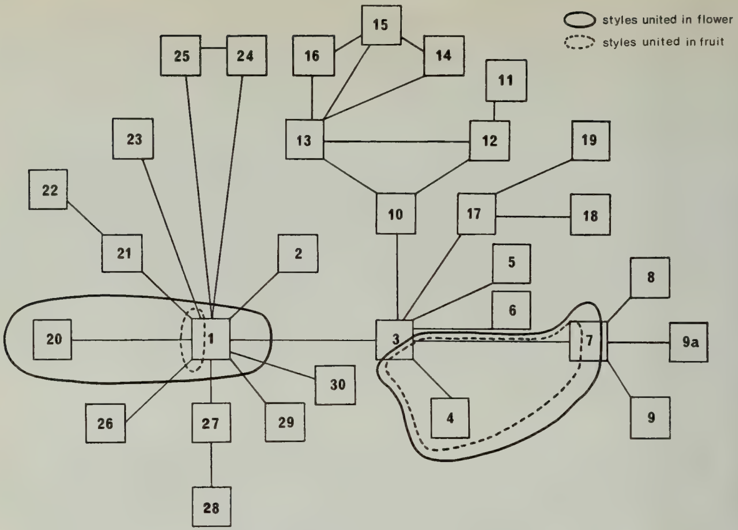

Fig. 22 Variation in stylar union in *Hypericum*.

(*g*) *Placentation*

The gynoecium in *Santomasia* and primitive species of *Hypericum*, as in the Bonnetioideae, consists of two parts: (i) a central columella comprising the five placentae and (ii) five curved peripheral parts of the ovary wall, which are united to each other and to the placentae by radial septa and are prolonged to form the styles. These septa are thin near the junction with the placentae, at the point where they separate from them in fruit (Fig. 23a; Maguire, 1972 : fig. 24j, k); and they are double structures, as is shown by their splitting longitudinally in fruit. In essence, therefore, the ovary comprises five curved valves (tegophylls—Melville, 1962) surrounding and alternating with five boat-shaped placental structures (sagittate in T. S.), which bear numerous ovules on both sides distally and approximate to one another more or less closely. The placentae are united towards the base; but above they are merely mutually appressed and may separate again towards the apex (Fig. 24a).

This state of placentation may be described as axile; but the loose association of the placentae makes a transition to true parietal placentation simple, and such a transition has occurred independently several times (Figs 23 h–k, 25). In other evolutionary lines the axile placentation has become more definite as a result of the more intimate union of the placentae (Figs 23c–g, 25). In some sections the placentation is wholly axile (e.g. in sects 17. *Hirtella* to 19. *Coridium*) (Figs 23c–e, 24a, b), in others it is constantly parietal (e.g in sects 29. *Brathys*, 30. *Spachium*) (Figs 23i–k, 24d), whilst a third group shows transitional stages (e.g. sects 20. *Myriandra*, 26. *Humifusoideum*) (Figs 23b, h, 24c). In sect. 5. *Androsaemum* the placentation remains axile at the base but becomes parietal almost abruptly above. Other trends have resulted in the gradual change of the columella element from a boat-shaped structure with an ovuliferous margin (Fig. 23a), by elimination of the sterile part, to a rod (Fig. 23e, k) or even a partial rod (Fig. 23g).

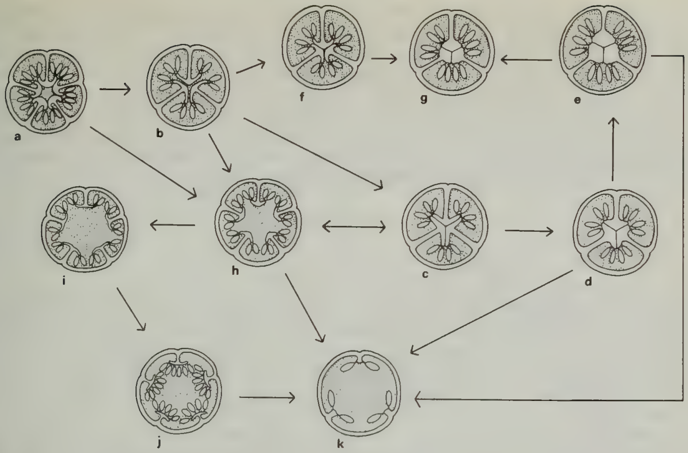

Fig. 23 Trends in placentation in *Hypericum* (T.S. of ovary *c.* 1/3 above the base) (diagrammatic): (a) *H. hookeranum*; (b) *H. olympicum*; (c) *H.* x *desetangsii*; (d) *H. montbretii*; (e) *H. empetrifolium*; (f) *H. cerastoides*; (g) *H. pulchrum*; (h) *H. papuanum*; (i) *H. rigidum*; (j) *H. brasiliense*; (k) *H. elodes*.

The arrows indicate overall trends, not relationship between the species illustrated.

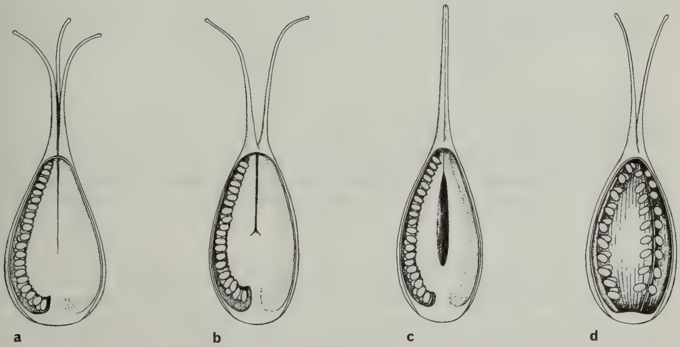

Fig. 24 Ovaries of *Hypericum* species in L.S. (diagrammatic) (numbers indicate sections): (a) *H. revolutum* (1); (b) *H. orientale* (16); (c) *H. prolificum* (20); (d) *H. elodes* (28) (a x 5; b x 7·5; c x 6·5; d x 8).

The placentation in the Vismieae and Cratoxyleae is basically similar to that described above. The fleshy fruit of the Vismieae is associated with thicker ovary walls and septa, whilst in the (capsular) Cratoxyleae the placentation is incompletely axile (*Cratoxylum*) or completely axile (*Triadenum*, *Thornea*) or axile with intrusive false septa (*Eliea*, cf. Baas, 1970). The Myrtaceae, as has already been stated, have a basically similar ovary structure to that of the Bonnetioideae and *Hypericum*, with the difference that the ovary is sunk in the receptacle and hence inferior. The fundamentally different, apocarpous gynoecium of the Dilleniaceae, however, makes one wonder if Corner (1976) was not correct in denying that there is a close relationship between this family and the Guttiferae.

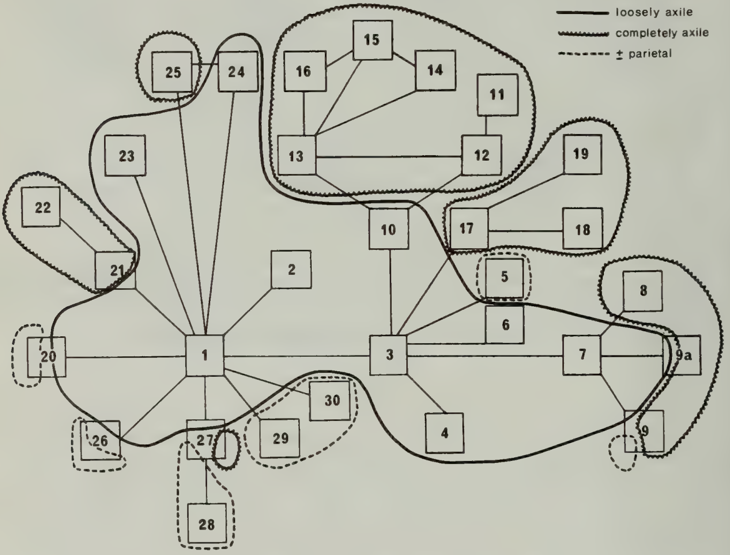

Fig. 25 Variation of placentation in *Hypericum*.

(*h*) *Ovules*

Each placenta margin in the primitive type of ovary is covered with numerous ovules, which vary in insertion from suberect near the apex to pendulous round the incurving base (Figs 23a, 24a). As the placentae become more parietal, the sterile region between their ovule-bearing margins diminishes and, when the placentation is wholly parietal, it disappears (Fig. 23k).

Dupuy & Guédès (1975) have described supernumerary axial ovules in two members of sect. 3. *Ascyreia*, viz. *H. calycinum* and *H.* x 'Hidcote'. These are four to six in number and occur on the top of the floral axis, i.e. *within* the placental region. They are vascularised from the stelar tissue remaining after the placental traces have departed. Dupuy & Guédès interpret these axial ovules as being foliar, not foliolar structures, i.e. they view them as representing an inner whorl of whole 'carpels', not extra ovules belonging to the placentae of the extant 'carpels'. According to the Gonophyll Theory, however, they terminate branchlets of a branch formed by a major dichotomy of the fertile branch of the gynophyll, the other major branch being the placental bundle, which vascularises the remaining ovules (see p. 141). Axial ovules have not been reported in any other species of *Hypericum*.

Another trend in *Hypericum* ovaries is towards a reduction in the number of ovules, a trend which roughly parallels the overall reduction in size. Extremes are reached in *H. thymopsis* (sect. 17. *Hirtella*) and *H. russeggeri* (sect. 25. *Adenotrias*), which have respectively 4–6 and 2 ovules per loculus. In the latter species one ovule is erect and the other pendulous (Jaubert & Spach, 1842–43 : t. 37).

The ovules are anatropous and bitegmic, as in the rest of the Guttiferae (Corner, 1976; Philipson, 1974, 1977), and tenuinucellate, as in most of that family, with the micropyle formed by the exostome (Corner, 1976).

Fruit

(*a*) *General*

In *Santomasia* and most *Hypericum* species the fruit is a somewhat woody or coriaceous septicidal capsule as in the Bonnetioideae but, unlike them, dehiscing at the apex, and usually with persistent valves. In four distantly related parts of *Hypericum*, however, a different type of fruit has evolved. In *H. olivieri* (sect. 17. *Hirtella*) the three ovary loculi are each 7–10-ovulate; but only one ovule usually matures into a seed, which is dispersed in the deciduous, subglobose, coccoid, capsule valve. Trends towards a baccate fruit have occurred thrice, but only one of them has resulted in the evolution of a true berry. In sect. 5. *Androsaemum* most of the species have a tardily and incompletely dehiscent capsule. *H. androsaemum* itself, however, has a fruit in which the pericarp is rather fleshy and colours during maturation to reddish-brown or black. *H.* × *inodorum*, of which it is a parent, shows similar but less extreme colour changes and is less succulent. Even in *H. androsaemum*, however, the 'berry' dries and can then be split into three valves with slight pressure from the fingers. The semi-fleshy fruits of *H. reptans* (sect. 3. *Ascyreia*) are even less baccate, but those of *H. peplidifolium* (sect. 26. *Humifusoideum*) are true berries.

In the Vismieae, true berries are characteristic of *Vismia* (many-seeded) and *Psorospermum* (5-seeded), whilst *Harungana* has a fleshy drupe with five several-seeded pyrenes. The genera of the Cratoxyleae all have apically dehiscent septicidal capsules except *Eliea*, where the development of false septa has resulted in a capsule with irregular dehiscence, partly septicidal partly loculicidal (Gogelein, 1967; Baas, 1970). The valves are more or less persistent except in some species of *Cratoxylum*, where they are caducous. In the other tribes and subfamilies of the Guttiferae the fruit is mostly indehiscent, except in the Clusieae, where it is capsular and loculicidal, and *Mesua ferrea* L., one of the more primitive species in the Calophylloideae, where the woody capsule also splits loculicidally.

(*b*) *Styles*

In many species the styles persist on the capsule, then wither and may break off irregularly (e.g. *Hypericum cerastoides*, sect. 11. *Campylopus*). Others have a zone of weakness near the base of the style, above which it withers and usually breaks off cleanly (e.g. *H. elongatum*, sect. 17. *Hirtella*). In both cases the capsule length will be measured from the base to the point of withering.

(*c*) *Vittae and vesicles*

As was mentioned above (p. 105), the ovary wall contains resin channels (vittae) which in *Santomasia* and some sections of *Hypericum* remain inconspicuous (e.g. in sects 1. *Campylosporus* and 29. *Brathys*), i.e. the capsule is 'not vittate' (Fig. 26a). In others (e.g. sects 9. *Hypericum* pro parte and 17. *Hirtella*) they become prominent in fruit as vertical raised lines, sometimes with superimposed glands (Fig. 26b). The next stage in this evolutionary trend is for the lateral vittae to become diagonal while the dorsal ones remain vertical (e.g. in *H. maculatum*, sect. 9. *Hypericum*) (Fig. 26c). The vittae may then become swollen (e.g. in *H. perforatum*, sect. 9. *Hypericum* or *H. perfoliatum*, sect. 13. *Drosocarpium*) (Fig. 26d) and break up into short streaks or dots ('vesicles') (e.g. in *H. montbretii*, sect. 13. *Drosocarpium*) (Fig. 26e). By comparison with its nearest relatives, *H. sampsonii* (sect. 9. *Hypericum*) seems to have evolved the vesiculate state directly from the vittate one; and in some species of sect. 30. *Spachium* (e.g. *H. pauciflorum*), one or two large vesicles develop on an otherwise smooth valve (Fig. 26g). Finally, although almost all these vittae and vesicles contain only amber resin, in *H. richeri* (sect. 13. *Drosocarpium*) some vesicles are blackish due to the presence of hypericin (Fig. 26f).

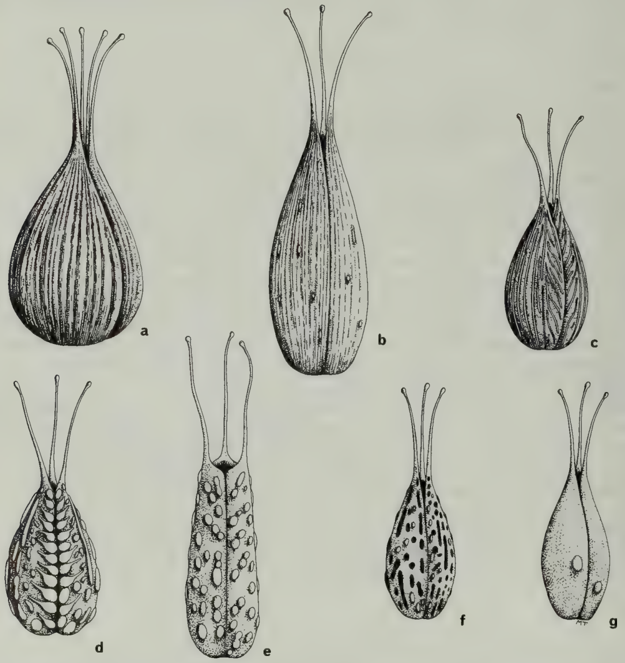

Fig. 26 Capsules of *Hypericum* species, showing patterns of vittae and vesicles (see text): (a) *H. revolutum* (1); (b) *H. elongatum* (17); (c) *H. maculatum* (9); (d) *H. perfoliatum* (13); (e) *H. montbretii* (13); (f) *H. richeri* (13); (g) *H. diffusum* (30) (all x 4).

Seeds

(*a*) *Number*

The number of seeds in a *Hypericum* capsule is sometimes very large (often well over 1000, cf. Salisbury, 1963); but trends in various groups have resulted in a reduction in number to the extremes found in *H. russeggeri* (sect. 25. *Adenotrias*) and *H. olivieri* (sect. 17. *Hirtella*), where only 6 and 3 seeds, respectively, are produced in each capsule.

(*b*) *Shape, size and colour*

The seeds in the Hypericoideae and Bonnetioideae, unlike those of the other Guttiferous subfamilies, are small and narrowly cylindric to ovoid-cylindric or ellipsoid. The longer ones may be slightly curved, especially if they are borne towards the base of the placenta; but this variation has no great taxonomic significance, despite the name of *Hypericum* sect. 1 (*Campylosporus*). In *Hypericum* they range from 1·5 mm long in *H. bequaertii* (sect. 1. *Campylosporus*) to 0·3 mm long in *H. gentianoides* (sect. 30. *Spachium*). They vary in colour from yellow-brown to red-brown or dark purplish brown.

(*c*) *Appendages*

Winged seeds occur in most Bonnetioid and Hypericoid genera with dehiscent fruit, usually in the more primitive members (e.g. in *Cratoxylum* but not in *Triadenum* or *Thornea*). Their apparently primitive status would seem to give support to Corner's (1976) theory that the wing is a vestigial arillar structure (true arils occur in the Clusieae). In some species (e.g. *Cratoxylum arborescens* (Vahl) Blume or *Mahurea casiquiarensis* Spruce) the wing surrounds the rest of the seed completely or almost so, in others (e.g. *Cratoxylum maingayi* Dyer) it is confined to one side, whilst in still others (e.g. *Ploiarium alternifolium* (Vahl) Melchior) it consists of terminal prolongations joined by little more than a carina. The two last-mentioned stages are found in *Hypericum**, but only in the more primitive sections (Fig. 27), the wing being thin and papery and thus unlike the cartilaginous wings with a peripheral vein that occur in *Cratoxylum* (Plate 1c).

Even if the wing has been reduced to a carina or less, the seed may have apical and sometimes basal prolongations (e.g. in *H. geminiflorum*, sect. 4. *Takasagoya*) or apiculi (cf. Plate 1b). In sect. 25. *Adenotrias* the basal apiculate expansion has evolved into a fleshy whitish

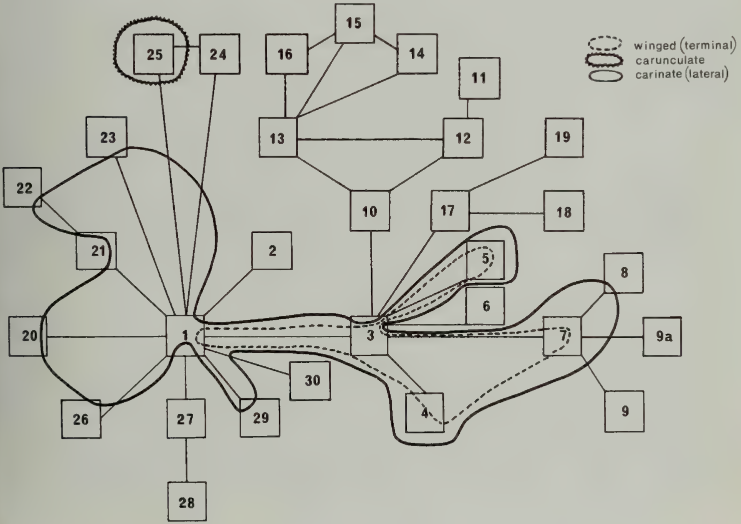

Fig. 27 Variation in seed appendages in *Hypericum*.

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*I have seen no seed of *Hypericum* with a complete marginal wing such as is illustrated by Keller (1925 : fig. 73P).

caruncle (Plate 2c). Although this change to specialised seed dispersal occurs in the very section that has evolved heterostyly, there is no obvious relationship between the two specialisations. No other *Hypericum* has a specialised means of seed dispersal (as opposed to fruit dispersal).

(*d*) *Testa sculpturing*

The seeds of *Hypericum* have the thick-walled stellate tegmen cells characteristic of all the Hypericoideae (except *Psorospermum*, where they are fleshy), as well as the Clusieae and probably the Bonnetioideae (Corner, 1976). The testa, however, is the part of the outer integument that provides characters that are infragenerically useful. Its inner layer is inconspicuous; but the cells of the outer epidermal layer have brownish to blackish tannin contents, and the radial and inner walls are more or less thickened (Ohlendorf, 1907). As the testa dries and matures, these thickened walls resist collapse, forming a reticulum of depressions in the testa; and the reticulate pattern so formed is sometimes characteristic of whole sections.

In the primitive state (e.g. in *Santomasia* and *Hypericum* sect. 1. *Campylosporus*) the exotestal cells form roughly defined lines and have relatively thin walls (i.e. the testa pattern is 'linear-reticulate') (Fig. 28 RE; Plate 1a–c). Three types of modification of this pattern can be observed:

(i) deformation of the lines of cells, making the testa merely 'reticulate', not 'linear-reticulate' (not differentiated in Fig. 28) (Plates 1d, 2b);
(ii) thickening of the lateral cell walls, often accompanied or preceded by lateral elongation of the cells (Plates 1e, 2d);
(iii) protrusion of the outer cell walls (Plate 2a).

Where thickening is confined to the longitudinal walls, the pattern becomes 'scalariform-reticulate', as for example in some species of sect. 30. *Spachium* (Rodríguez-Jíménez, 1974 : plate 2b, c) (Fig. 28S–RE; Plate 2e). Where this longitudinal thickening has become more pronounced, so that the seed looks ridged, the pattern is termed 'ribbed-scalariform' (Rodríguez-Jiménez, 1974 : plate 2a) (Fig. 28RI–S; Plate 2d).

Where all the walls are thickened, so that the depression between them is round, the testa is 'foveolate' or 'linear-foveolate', a common state in *Hypericum* (Fig. 28FO; Plate 1f). Where the outer cell walls of a foveolate testa have begun to protrude, a 'rugulose' pattern is produced (in sects 12, 18–19, 22) (Fig. 28RU; Plate 2c); and more pronounced protrusion results in a 'papillose' testa (in sects 17–19) (Fig. 28PA; Plate 2a). The apparent absence of rugulose seeds from sect. 17. *Hirtella*, which in other characters is basic to sects 18–19, suggests that they probably occurred in the basic stock from which these three sections evolved, but that the trend to papillose seeds was established earlier in sect. 17. *Hirtella* than it was in the other two sections.

(*e*) *Embryo*

Although seeds of the Guttiferae are usually said to be exalbuminous, Corner (1976) points out that a layer 1–2 cells thick of nuclear oily endosperm is present in the Hypericoideae and sometimes in the other subfamilies, and that it may not be completely absent in *Ploiarium* (Bonnetioideae). Prakash & Lau (1976), however, make no mention of it in their paper on *P. alternifolium*.

The embryo in *Hypericum*, as in the Bonnetioideae and other Hypericoideae except *Psorospermum* (Vismieae), is slender and straight with equal, plano-convex cotyledons which are somewhat shorter than the hypocotyl. In *Psorospermum* the seeds are reduced in number to one in each loculus of the 5-locular baccate fruit and are much larger than in the ancestral *Vismia*; and in the embryo the cotyledons vary in the three subgenera from equal, symmetric and accumbent (subgen. *Psorospermum*) to either unequal, asymmetric and incumbent (subgen. *Parasorospermum*) or equal and inrolled to conduplicate (subgen.

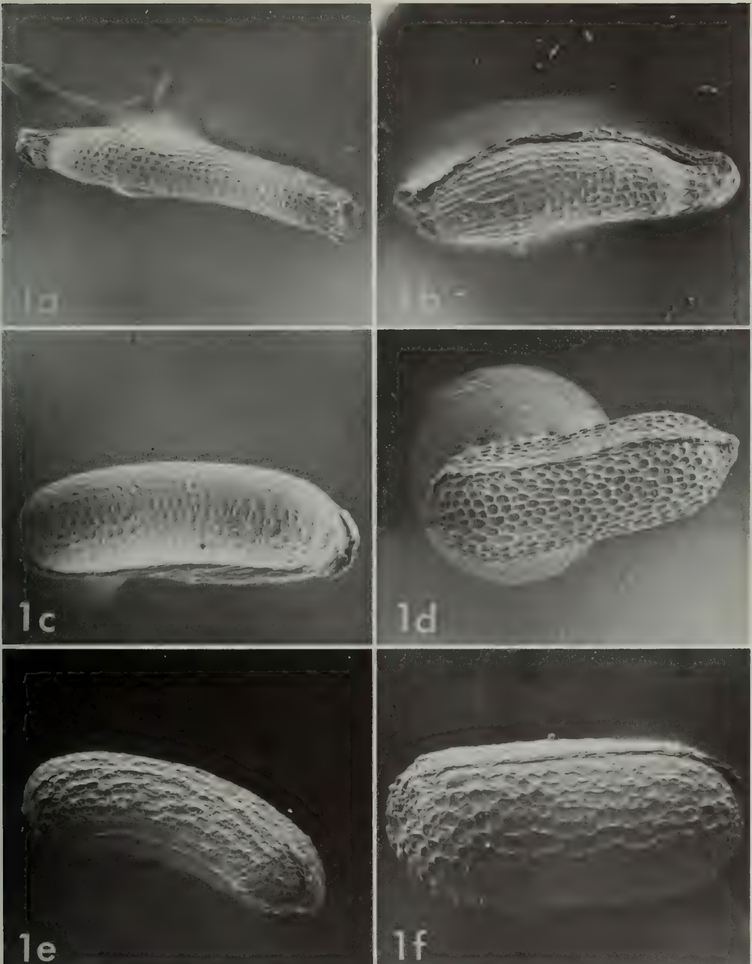

Plate 1 Seeds of *Hypericum*, I (numbers indicate sections): (a) *H. revolutum* (1); (b) *H. acmosepalum* (3); (c) *H. ascyron* (7); (d) *H. maculatum* (9); (e) *H. richeri* (13); (f) *H. linarifolium* (14) (a x 46, b x 53, c x 51, d x 55, e x 46, f x 90).

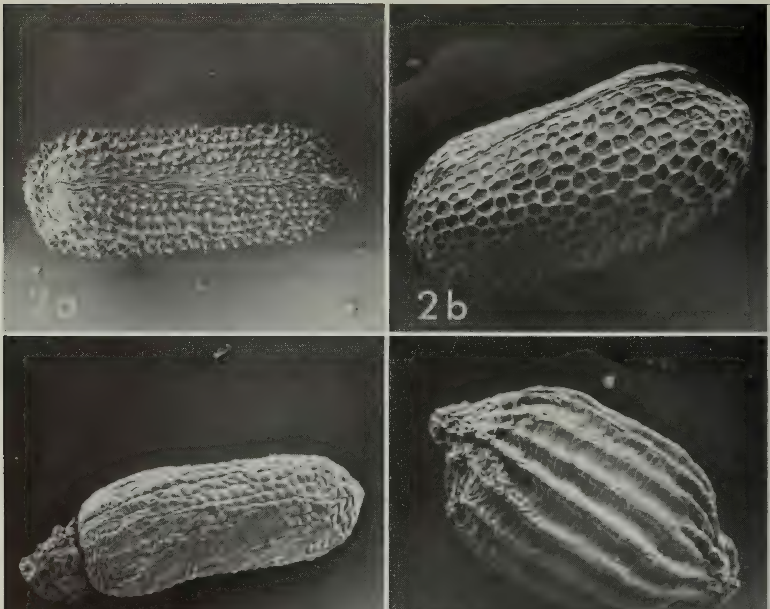

Plate 2 Seeds of *Hypericum*, II (numbers indicate sections): (a) *H. hirsutum* (18); (b) *H. hypericoides* (20); (c) *H. aegypticum* (25); (d) *H. elodes* (28); (e) *H. moranense* (30); (f) *H. mutilum* (30) (a x 60, b x 63, c x 40, d x 75, e x 130, f x 110).

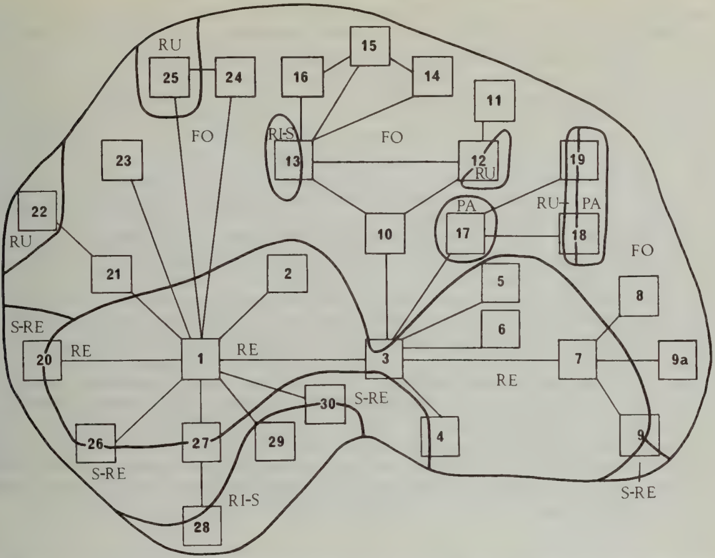

Fig. 28 Variation in seed testa in *Hypericum*: FO foveolate, PA papillose, RE reticulate, RI-S ribbed-scalariform, RU rugulose, S-RE scalariform-reticulate.

Afropsorospermum) (Bamps, 1966). According to Vestal (1938), the cotyledons are longer than the hypocotyl in the Vismieae and Cratoxyleae, but shorter than it in the Hypericeae. In the other subfamilies of the Guttiferae the embryo structure varies widely and becomes highly specialised (cf. Brandza, 1908).

4. Pollen morphology

By G. C. S. Clarke

Introduction

This is a summary of a more extensive paper on the pollen morphology of the genus *Hypericum* which will, it is hoped, appear in this journal in due course. To avoid repetition, most of the details and the illustrations have been omitted from the present account; they will be found in the main paper.

The pollen grains described here have been studied by means of the light microscope and the scanning electron microscope, after preparation by the standard acetolysis technique as refined by Reitsma (1969). The pollen samples have all been taken from herbarium specimens which will be listed in the main account. About 250 species have been examined.

General description

The standard pollen type throughout the genus is tricolporate with a microreticulate or reticulate pattern of ornamentation. Pollen of this kind is common throughout the dicotyledonous angiosperms, so *Hypericum* pollen is not particularly distinctive and there is little evidence from pollen morphology for the discreteness of *Hypericum* as a genus. Some genera of the Guttiferae are more distinct in their pollen morphology (Clarke, 1975); a few have porate rather than colporate grains and a few are characterised by having more than three apertures.

The only divergence within the genus *Hypericum* from the standard tricolporate plan is the tendency for some species to produce pollen grains with more than three apertures, and in which the strict polarity of the standard grains has disappeared. There is circumstantial evidence that this phenomenon is linked with cytological factors that influence meiosis (Clarke, 1975). In many of the species where they occur, the irregular grains form only a small proportion of the total, but in a few species practically all the grains are of the irregular type. This is discussed below (see pollen type XI).

A generalised description of the features common to the pollen grains of all the *Hypericum* species I have seen is as follows (terminology according to Erdtman, 1971; Faegri & Iversen, 1975; Reitsma, 1970):

Pollen tricolporate, spheroidal to prolate. *Outline* in polar view more or less circular to three-lobed with the apertures set between the lobes, or triangular; in equatorial view elliptic, rectangular-elliptic or rhombic. *Ectoapertures* colpi, long to very long, parallel-sided or, more often, widest at the equator; often partly covered at the equator by sexine extensions; margin sometimes thickened near equator; colpus membrane smooth or granular. *Endoaperture* a lalongate colpus, porus or lolongate porus, sometimes with short lateral extensions; margins often thickened across colpus membrane. *Exine* usually rather thin, nexine about as thick as sexine; columellae short, unbranched. *Ornamentation* microreticulate, reticulate or a tectum perforatum; muri often broader at the base than above, simpli- or duplicolumellate; lumina irregular in outline, sometimes enclosing free columellae. *Size*—Polar axis 13–45 μm; equatorial diameter 7–28 μm.

Variations in pollen morphology

Within the basic morphological scheme outlined above there is sufficient variety for eleven pollen types to be described. The types have been numbered from I to XI but there is no special significance in the numbering and it is not intended to imply a morphological or evolutionary sequence. The diagnostic characters of the types are as follows:

Pollen type I: Grains prolate-spheroidal to subprolate. *Endoaperture* a porus with very small lateral extensions. *Ornamentation* a tectum perforatum or microreticulum; tectal perforations regularly spaced.

Pollen type II: Grains prolate-spheroidal to subprolate. *Endoaperture* a porus, often more or less lalongate, with very small lateral extensions. *Ornamentation* a tectum perforatum or microreticulum; tectal perforations grouped together.

Pollen type III: Grains subprolate. *Endoaperture* a lalongate colpus. *Ornamentation* a tectum perforatum or microreticulum; tectal perforations grouped together.

Pollen type IV: Grains subprolate. *Endoaperture* a lalongate colpus. *Ornamentation* a tectum perforatum or microreticulum; tectal perforations regularly spaced.

Pollen type V: Grains spheroidal or prolate-spheroidal. Outline in polar view triangular with concave sides. *Endoaperture* a lalongate colpus. *Ornamentation* a tectum perforatum or microreticulum; tectal perforations regularly spaced.

Pollen type VI: Grains perprolate or prolate. *Endoaperture* a large porus, more or less circular or lolongate. *Ornamentation* microreticulate or reticulate; lumina regularly spaced.

Pollen type VII: Grains very small, prolate. *Endoaperture* a large lolongate porus. *Ornamentation* microreticulate or reticulate; lumina regularly spaced.

Pollen type VIII: Grains prolate. *Endoaperture* a very large lolongate porus or colpus. *Ornamentation* reticulate and microreticulate; lumina regularly spaced.

Pollen type IX: Grains very large, subprolate or prolate. *Endoaperture* a more or less lalongate porus with short lateral and meridional extensions. *Ornamentation* reticulate; lumina regularly spaced.

Pollen type X: Grains prolate or subprolate. *Endoaperture* a more or less lalongate porus with short lateral and meridional extensions. *Ornamentation* microreticulate; lumina regularly spaced.

Pollen type XI: Grains all of irregular form and variable shape. Apertures varying in number from 2 to 12; arranged in many different ways.

Discreteness of the pollen types

Some of the eleven pollen types are very distinct and there is no difficulty in separating them from all the others. Examples of this are types V, VI, VII, VIII and IX. Some types are distinct in the majority of cases, but exceptional specimens may link them with other types. Thus type II is normally very distinct, but a few species have pollen grains which are morphologically intermediate between types II and I. Similarly, some species are intermediate between types III and IV. Types I, IV and X can also be hard to separate because the structure of the endoaperture is difficult to observe.

Type XI is anomalous since it is defined on different criteria from the other types. Its recognition depends on the presence of an overwhelming proportion of irregular pollen grains in a specimen. In effect, what this means is that when a species does not produce normal pollen grains it cannot be categorised in the same way as other species. Some species of other types, notably II and X, produce a small proportion of irregular grains, but the remaining grains can be assigned to a type in the normal way (Clarke, 1975).

Distribution of the pollen types amongst the sections

The level at which pollen morphology relates to taxonomy in the genus *Hypericum* corresponds most closely to the section. Table 5 and Fig. 29 show how the pollen types are distributed amongst the 31 sections of the genus recognised by Robson. The species of some sections all have pollen of a single type (sects 20. *Myriandra*, 28. *Elodes* and 25. *Adenotrias* are examples of this), while those of other sections, notably sect. 3. *Ascyreia*, are divided between several types. In the same way, some of the pollen types, such as II or V, are found exclusively in species from a single section, while others, such as III, IV or particularly X, are found in a number of sections. In one or two cases the majority of the species in a section fall into one pollen type, but one or two species are anomalous and have pollen of another type. Sect. 9. *Hypericum* is a case in point: all the species I have examined fall into type X with the exception of *H. epigeium*, which has pollen of type IV. This kind of distribution pattern remains unexplained.

Relationships between the pollen types

The morphology of the eleven pollen types suggests that they can be grouped together in a way that may reflect relationships between them. Four main groups can be formed. The first group includes pollen types I and II, which have a similar form of endoaperture. The second brings together types III, IV and V, which are again linked by the form of their endoapertures. The third includes types X, IX and XI, of which IX and XI seem to be specialisations derived from X. The fourth group combines types VI, VII and VIII; types VII and VIII, with their large endoapertures and characteristic ornamentation, seem more closely linked to each other than either is with type VI, which shares some features with them and other features with type I.

Table 5 Distribution of the pollen types amongst the sections of *Hypericum*

Sections	Pollen types										
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Campylosporus	+										
Psorophytum				+							
Ascyreia	+	+	+	+							
Takasagoya			+								
Androsaemum			+	+							
Inodorum			+								
Roscyna			+								
Bupleuroides				+							
Hypericum				+						+	
Concinna										+	
Olympia										+	
Campylopus										+	
Origanifolia				+							
Drosocarpium										+	
Oligostema										+	
Thasia										+	
Crossophyllum										+	
Hirtella										+	+
Taeniocarpium										+	
Coridium										+	
Myriandra							+				
Webbia	+										
Arthrophyllum	+			+							
Triadenioides				+		+					
Heterophyllum										+	
Adenotrias					+						
Humifusoideum										+	
Adenosepalum	+									+	
Elodes									+		
Brathys								+			
Spachium								+			

The distribution of morphological characters within these four groups suggests that there may be a sequence from the first group, the most primitive, to the fourth which is the most advanced. The arguments in favour of this conclusion will be developed in the main paper.

Taxonomic implications of the pollen morphology

Although every species in the genus has pollen which is constructed on a basically similar pattern, the variations described here suggest a number of taxonomic conclusions. Only the most general of these will be summarised here.

1. Only in exceptional cases does pollen morphology contradict the way the genus has been subdivided into sections by Robson.
2. Sect. 1. *Campylosporus* seems to contain the species with the most primitive pollen.
3. Sects 29. *Brathys* and 30. *Spachium* contain the species with the most advanced pollen. They have a good deal in common with sect. 20. *Myriandra*, but with few others.
4. Sect. 3. *Ascyreia* is morphologically rather variable, since it brings together species with four different pollen types.
5. There are a large number of sections which are apparently closely related since all the species they include have pollen of type X.

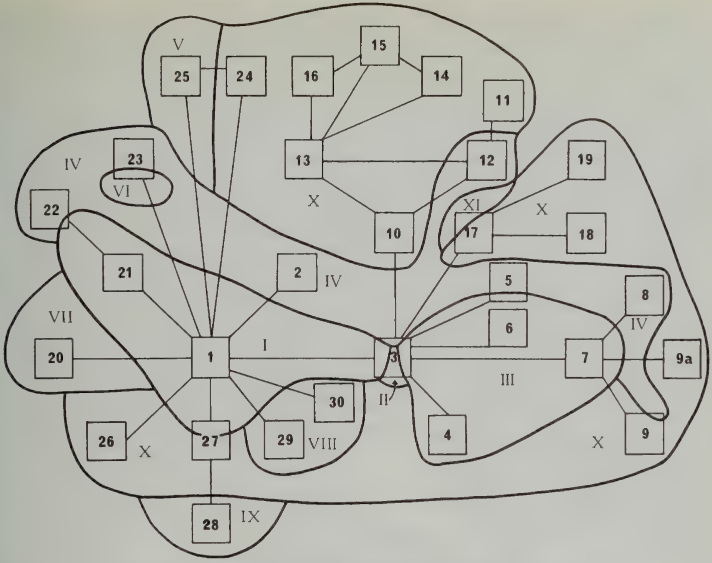

Fig. 29 Distribution of pollen types in *Hypericum* (see text).

5. Biology of flower and fruit

Pollination

(a) Unspecialised flower

The flowers of *Hypericum* are probably all nectarless and open to visitation by any insects. They are therefore typical 'pollen flowers' with relatively numerous stamens. The petals have no honey guides or strong odour that might attract insects, although the whole plant sometimes gives off an aromatic scent in hot weather. This is frequently reminiscent of curry (e.g. the South African name for *H. revolutum* (sect. 1. *Campylosporus*) is Curry Bush—Killick & Robson, 1976); but it may be the less pleasant 'he-goat' aroma of *H. hircinum* (sect. 5. *Androsaemum*). The latter is due to caproic acid (n-hexanoic acid) or caprylic acid (n-octanoic acid). For these reasons the flowers of *Hypericum* are relatively primitive; and further primitive characters are (i) the prevalent yellow colour of the petals and inner organs and (ii) the homogamy and apparent self-compatibility of most species.

The flowers of species such as *H. kouytchense* (sect. 3. *Ascyreia*) are of the type described by Faegri & van der Pijl (1971) as primitive brush blossoms (Fig. 30a). In such flowers the numerous stamens provide a platform over which the insect visitor moves, the anthers brushing against the underside of the insect's body and transferring pollen to it. This pollen is then deposited by the insect on an adjacent stigma or on one in another flower.

The 'platform' is produced by the gradual inward movement of the stamens as the anthers dehisce, starting with the innermost ones, which in nearly all species are the shortest. As these do not attain the level of the stigmas, cross-pollination is favoured. In *H. calycinum* and some other *Hypericum* species with relatively primitive flowers, the differentiation of height is not great; but in the more advanced flower of *H. perforatum*, for example, it is considerable (Fig. 30b). This relationship between stamen length and stigma level (i.e. style + ovary length) appears to exist in most open-pollinated species of *Hypericum*. In some 'wide' hybrids (e.g. *H.* x *moseranum* Luquet ex André and *H.* 'Hidcote', both sect. 3. *Ascyreia*), however, the anthers do not ever reach the level of the stigmas, which indicates that the mating of two species with distinct floral structures has resulted in biological disfunction (quite apart from any genetical or chromosomal disfunction that has occurred). A second exception is found in at least some species of sect. 29. *Brathys* (e.g. *H. laricifolium*), in which the stamens fall far short of the stigmatic level. From the observation that the filaments in such flowers are rather thick and crumpled, however, it would seem that they have undergone some sort of contraction, possibly associated with self-pollination at anthesis.

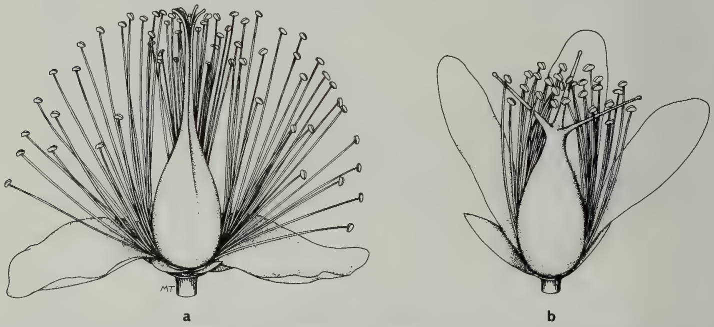

Fig. 30 Pollination of unspecialised *Hypericum* flowers (one sepal and two petals removed): (a) *H. calycinum* (x 2·5); (b) *H. perforatum* (x 4).

As the outer stamens move inward, the anthers come into contact with the stigmas, thus ensuring self-pollination if cross-pollination has not occurred (Fig. 30b). In some species (e.g. *H. linarifolium* and *H. humifusum*, sect. 14. *Oligostema*), unfavourable weather conditions result in pseudocleistogamy, i.e. the flowers do not open and are automatically self-pollinated (Ivimey-Cook, 1963). The styles in bud are erect and in contact with the anthers. In primitive species they remain erect or more-or-less united, so that no movement is necessary for self-pollination to occur, other than a slight outcurving at the tip. In several sections (e.g. 10. *Olympia*) the petals close up as well as the stamens, resulting in a second bud-like stage of anthesis. This movement, however, does not appear to be necessary to ensure self-pollination (although it may help to produce it), as the species in which the petals and/or stamens are deciduous (e.g. in sect. 3. *Ascyreia*) are not noticeably less fertile, under similar conditions, than those with a second bud-stage.

(*b*) *Insect visitors*

Such flowers as those that have just been described are typically visited by the less-specialised insects, of which the Syrphidae (Diptera) are the commonest visitors to *Hypericum*. They are particularly associated with yellow flowers (Faegri & van der Pijl, 1971), and the well-known irregularity of their visits may have been a factor in the evolution (? or retention) of a self-compatible breeding system. Bombylids, which are also frequent visitors, are more specialised; but they commonly visit primitive flowers for pollen. Müller (1883), moreover, observing that these flies frequently put their tongues into the flowers of

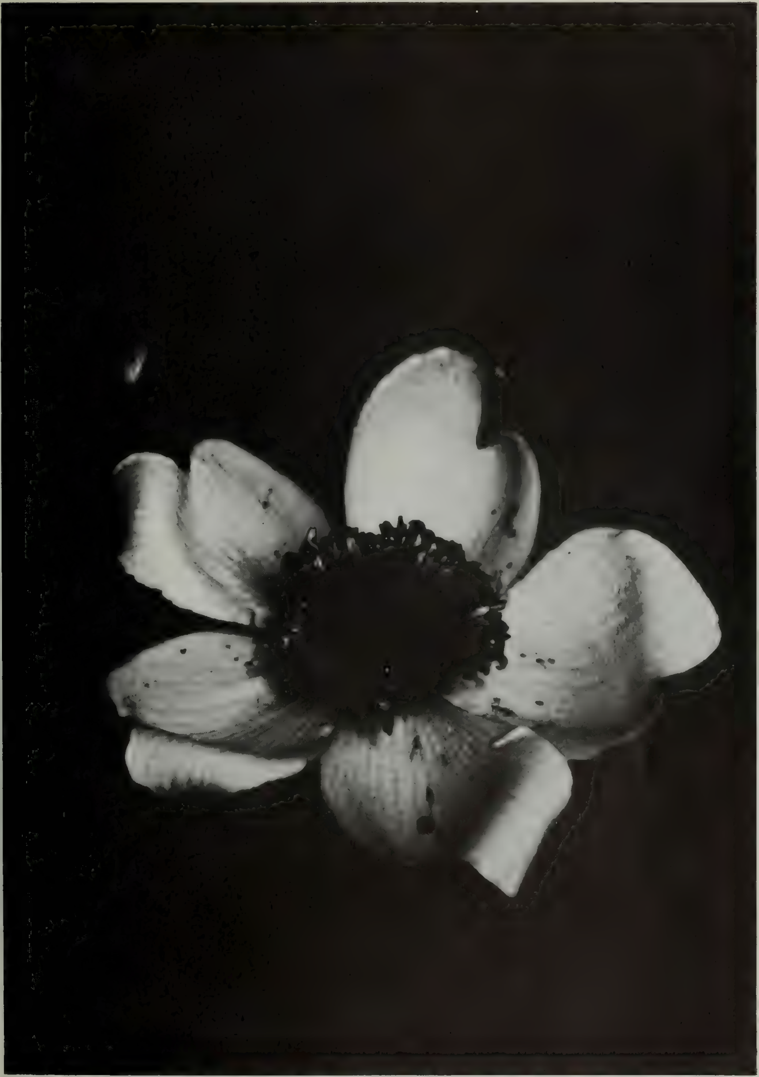

Plate 3 *H.* 'Hidcote', photographed in ultraviolet light to show the 'bull's-eye' (bee-yellow) at the centre of the flower and the contrasting outer (bee-purple) region.

H. perforatum, suggested that they were boring into the soft tissues. They would thus obtain sap but not, of course, nectar.

For lists of specific insect visitors, the reader is referred to Knuth (1908) and Faegri & van der Pijl (1971).

The aromatic scent characteristic of some species of *Hypericum* may, as has been stated, attract insect visitors to the vicinity of the plant; but the attraction of the flowers themselves is probably wholly visual. There is no internal contrast to the yellow colour, such as would be provided by e.g. honey guides; but the anthers are sometimes darker yellow to orange (e.g. in *H. hookeranum*, sect. 3. *Ascyreia*) and rarely may be reddish (*H. calycinum*, sect. 3. *Ascyreia* and *H. pulchrum*, sect. 18. *Taeniocarpium*). The colour contrasts are on the outside of the petals, in the form of red tinges or veining, which are invisible when the flower has opened. In bud, however, they are conspicuous. As they are confined to that part of each petal that is exposed, the whole bud appears dark red or red-veined. Eisner *et al.* (1973) have shown that these red patterns appear dark in ultraviolet light, in contrast to the rest of the outside of the petal. The centre of the open flower (petal bases, stamens, ovary) is also ultraviolet-dark, although it is not differently coloured to the human eye in normal light. To the visiting insect, however, the open flower is a 'target', with a yellow 'bull's-eye' surrounded by 'bee-purple' (Plate 3). The unopened buds, in contrast, are wholly yellow and therefore less attractive from a distance. As these also differ in form from the open flowers, insects would have little difficulty in distinguishing and avoiding them.

(*c*) *Floral specialisation*

In the species with large flowers the single flower is the pollination entity (Faegri & van der Pijl, 1971); but, in more advanced species, reduction in size is accompanied by various degrees of aggregation. As there is a parallel reduction in the number of stamens in each flower, this floral aggregation will tend to retain an efficient 'brush' pollination mechanism. The most extreme aggregation is found in two species of sect. 30. *Spachium* from Uruguay and adjacent Brazil and Argentina, *H. myrianthum* and *H. tamariscinum* Cham. & Schlecht. (= *H. notiale*, *H. pelleterianum*), where the very small flowers are in a dense flat corymb. *H. scabrum* (sect. 17. *Hirtella*) has dense flat corymbs of larger flowers, whilst in the closely related *H. capitatum* the dense inflorescence is broadly pyramidal to capitate.

Another specialisation concerns the styles, which, as we have seen, are erect with outcurved tips in the primitive species. In all evolutionary lines there is a tendency for the styles to spread more widely, and this is most noticeable in the sections (e.g. 9. *Hypericum*) where there are 'three' stamen fascicles. Here the three styles diverge from the base *between* the fascicles, favouring cross-pollination, only later assuming a more erect position that allows the longer (outer) stamens to close up and effect self-pollination. In sections where the stamens are irregularly distributed (e.g. 30. *Spachium*), the relation between the positions of style and stamens is less close, as it also is in those sections with transitional floral structure (e.g. 5. *Androsaemum*: 5 fascicles, 3 erect styles; 8. *Bupleuroides*: '3' fascicles, 3 erect styles). In sect. 20. *Myriandra*, where the fascicles have merged completely, the styles are completely appressed except in the more advanced species with a tetramerous perianth, where they eventually curve at the apex.

In the two sections where specialised pollination occurs (sects 25. *Adenotrias* and 28. *Elodes*), the character syndrome in the flowers of each section is remarkably similar (Robson, 1972*a*). In both, the sepals remain stiff and erect, so that the petals can spread out distally only. The corolla is thus pseudotubular; and, correlated with this development of a 'corolla tube', the filaments in each stamen fascicle have become united to above the middle (Fig. 31). The petals have evolved a ligulate outgrowth (entire in *Adenotrias*, trifid in *Elodes*) which has juicy tissue in its axil and may be a source of nectar, although I have not observed free nectar in either *H. aegypticum* or *H. elodes*. In *H. aegypticum*, however, the ligule is appressed to the ovary by the development of a wedge of connecting tissue. The space between adjacent wedges forms a groove that would guide a probing insect tongue towards

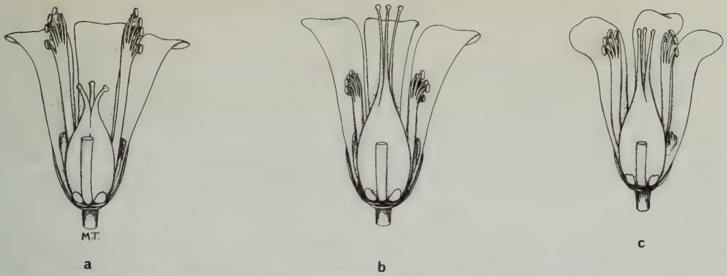

Fig. 31 Pollination of specialised *Hypericum* flowers (one sepal and two petals removed): (a) *H. aegypticum* (short-styled); (b) *H. aegypticum* (long-styled); (c) *H. elodes* (homostyled) (all x 4).

the base of the ovary, where it would be deflected laterally to a space between two of the three hypogynous 'scales'. These are entire in *Adenotrias*, bilobed in *Elodes*; and, whatever their morphological status may be (see p. 102 and Robson, 1972*a*), these act as lodicules, by swelling during development, thus helping to expand the flower (Hochreutiner, 1918). The three styles diverge so that the stigmas are between the 'three' fascicles and would be encountered by a pollen-laden probing insect.

H. aegypticum and the other species in sect. *Adenotrias* are more highly evolved than *H. elodes* in exhibiting diheterostyly (Fig. 31a, b), combined, at least in *H. aegypticum*, with a moderately strong incompatibility system (Ornduff, 1975). Ornduff has shown that there is a good reciprocal correspondence between the positions of anthers and stigmas of the 'pin' and 'thrum' forms of the flower, and that the pollen grains too are dimorphic. Those from anthers of 'thrum' flowers are on the average considerably larger than those from 'pin' flowers. In addition, 'pin' flowers produce an average of 1·7 times as many pollen grains as do 'thrum' flowers. Self-pollinations and own-form-pollinations produced 31·6–47·5% fruit-set and an average of 2·7–5·8 seeds per pollination, whereas the corresponding figures for other-form-pollinations were 83·3–100% and 23·9–27·0 respectively.

Breeding systems

Relatively little information is available on breeding systems in *Hypericum*. Self-compatibility is apparently widespread in the genus but not universal. The moderately strong incompatibility system in *H. aegypticum* has just been discussed; and Salisbury (1963) has discovered one in *H. calycinum* (sect. 3. *Ascyreia*). The latter, he suggested, is due to (i) degrees of failure in embryo development and (ii) inefficient endospermic nutrition during the attainment of the resting stage. Myers (1963), however, found *H. calycinum* and various other species and hybrids of *Hypericum* and *Triadenum* all to be pollen-tube/style compatible; and Culwell (1970), while reporting that the eastern North American species of sect. 9. *Hypericum* were all self-fertile, suspected that at least some of them might be pseudogamous (see p. 172).

The flowers of *Hypericum*, like those of other genera of the Hypericoideae, are bisexual, and specialisation in this subfamily tends towards heterostyly, not dioecy. The occurrence of pistillody of the stamens in *H. nudiflorum* (sect. 20. *Myriandra*) reported by Rehder (1911) is no doubt, therefore, due to an isolated genetical aberration and is not an indication of an evolutionary trend. For other breeding aberrations, see 6. Development (p. 125).

Seed dispersal

(*a*) *Gravity*

Seeds of *Hypericum* species are cylindric to ellipsoid, small (about 0·3–1·5 mm long) and light (those of native and naturalised British species range from 0·00002 to 0·00058 g on average—Salisbury, 1942, 1963); and they are usually shed from the plant by the septicidal dehiscence of a capsule. Although they are small and light, they are not sufficiently so to be dispersed for long distances by wind without morphological adaptation—which most of them do not appear to have. The majority of seeds, therefore, fall near the parent plant.

(*b*) *Wind*

Although most seeds have no morphological adaptation for wind-dispersal, those of the more primitive species have a prominent carina or a narrow unilateral membranous wing or terminal appendage (e.g. in sect. 5. *Androsaemum*). No observations have been published that show these to be effective in wind-dispersal, but they may be expected to assist it to a limited extent. On the other hand, Ridley (1930) cites records of *H. hirsutum* (sect. 19. *Taeniocarpium*) and *H. perforatum* (sect. 9. *Hypericum*) growing on walls at about 6 m above the ground, well above the raindrop splash-zone; and so even wingless seeds may be carried for short distances by wind; Salisbury (1952) states without further comment that the (unwinged) seeds of *H. montanum* (sect. 27. *Adenosepalum*) are dispersed by wind, as does Ivimey-Cook (1963) for *H. linarifolium* (sect. 14. *Oligostema*).

(*c*) *Water*

H. elodes (sect. 28. *Elodes*) grows in damp mud or water and can flower where the water is not too deep (Glück, 1911). In shallow water, when the capsules dehisce in August, the seeds float on the surface for about three days and can be dispersed by waves (Ohlendorf, 1907). Subsequently they sink and overwinter in the mud at the bottom, the sclerotic layer of the testa preventing their rotting.

(*d*) *Animals (external)*

(i) Birds. Many species of *Hypericum* besides *H. elodes* grow in damp mud, and their seeds might therefore be expected to adhere to the feet or feathers of wading birds and waterfowl. *H. elodes* has a limited seed-production, so that its occurrence in ponds that become dry is probably due to vegetative dispersal by ducks (Ridley, 1930). Other species of damp habitats are mostly herbs belonging to sect. 30. *Spachium* (e.g. *H. canadense*), and it is significant that this section is the only one in the genus to show evidence of long-distance dispersal. In contrast to *H. elodes*, such plants of lake- or riverside or marsh are probably propagated wholly by seed. Several North American members of this section have been found in scattered localities in Europe and western Asia (Caucasia) in the last 150 years or so (Gorshkova, 1949; Heine, 1962), and, although relict status (i.e. perglacial survival) has been proposed as the most likely explanation of the occurrence of *H. canadense* in Ireland (Webb, 1958), the generally haphazard European distribution of these species suggests that carriage of seed by wading birds or waterfowl is the most likely explanation of their isolated occurrences. The existence of wide disjunctions elsewhere in the section (see p. 206 and Robson, 1977*a*) provides supporting evidence for this hypothesis. Of course, accidental human introduction cannot be ruled out in some cases (cf. Webb & Halliday, 1973). There is, however, a complete absence of direct evidence of bird-transport (no seeds of these species have been found on migratory birds, for example), but the circumstantial evidence is strong.

(ii) Mammals. The absence from *Hypericum* seeds of adaptations favouring adherence to wool or hair indicates that mammals are not likely to be effective dispersal agents. There is one record of *H. triquetrifolium* (sect. 9. *Hypericum*) growing on wool-heaps in Montpellier (Thellung, 1912); but it is more likely, with such a divaricately branched species, that the whole fruiting plant (or part of it) adhered to the wool than that the seeds alone were transported.

(iii) Insects. In the seeds of *Hypericum aegypticum* and the other species in sect. 25. *Adenotrias*, the terminal appendage has become a hard white caruncle. No doubt this is attractive to ants, which are therefore likely to aid the dispersal of these species.

(*e*) *Animals (internal)*

In three sections of *Hypericum*, as was mentioned above (p. 109), the capsule has evolved a fleshy wall and become tardily dehiscent or indehiscent. There are no recorded field observations on *H. reptans* (sect. 3. *Ascyreia*) or *H. peplidifolium* (sect. 26. *Humifusoideum*) to show which animals utilise these berries as food, and neither species has relatives with tardily dehiscent fruit.

In sect. 5. *Androsaemum*, however, the first stages in the evolution of a berry are seen in *H. hircinum*, where the fruit, although capsular and persistent, is incompletely dehiscent. In *H. androsaemum* the fruits ripen to a shiny berry (black or dark red-brown), which is easily detachable from the receptacle. If not eaten, after about a month they dry and can be split into three valves by relatively slight pressure. The seeds are then, according to Ridley (1930), dispersed by wind and rain. The fruits have been described as deciduous, but I have never seen one falling from the plant and believe that naked receptacles are always due to removal of the fruit by birds (cf. Robson, 1973*b*). Ridley (1930) reported that a clump that he kept under observation at Kew showed no signs of having been visited by these animals, but the spread of *H. androsaemum* in New Zealand (where it was introduced) has been attributed to their activities (Thomson, 1922; Connor, 1977). My own observations of its propensities to become a garden weed in various parts of Britain suggest that it is being spread by birds, although I, too, have failed to observe a bird eating the fruit of this species or its hybrid with *H. hircinum* (*H.* x *inodorum* Miller).

6. Development

Embryology

(*a*) *Normal form*

The first paper completely devoted to *Hypericum* embryology was that by Schnarf (1914), whose study on *H. calycinum* (sect. 3. *Ascyreia*), *H. perforatum* and *H. maculatum* (sect. 9. *Hypericum*) was followed by those of Palm (1922) on *H. japonicum* (sect. 30. *Spachium*), Souèges (1925) on *H. perforatum*, Hoar & Haertl (1932) on some North American species in sects 9. *Hypericum*, 20. *Myriandra* and 30. *Spachium* (as well as *Triadenum virginicum* (L.) Rafin.), Souèges (1936) on *H. tetrapterum* (sect. 9. *Hypericum*), Swamy (1946) on *H. mysurense* (sect. 3. *Ascyreia*), Govindappa (1956) on *H. japonicum*, and Rao (1957) on '*H. patulum*' and *H. mysurense*. Various sections of the genus have therefore been examined; and the account given by Davis (1966) summarises the findings of these and other authors. There is apparently no variation that could be of taxonomic value within *Hypericum* itself, but such differences occur between the Hypericeae and other tribes.

In *Hypericum* the anther is bisporangiate, whereas it is tetrasporangiate in *Ploiarium* (Prakash & Lau, 1976). The microspore tetrads are tetrahedral, isobilateral or decussate, and the pollen grains are 2-celled when shed. The ovule in *Hypericum*, as in *Ploiarium* (Prakash & Lau, 1976), is anatropous, bitegmic and tenuinucellar, with the micropyle formed by both integuments. The archesporial cell functions directly as the megaspore mother cell, and a linear tetrad develops into a *Polygonum*-type embryo sac.* The three

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*In contrast, the tetrad may be T-shaped in *Triadenum* (Myers, 1963), in genera of other Hypericoid tribes and in *Ploiarium*; and in *Camellia* (Theaceae), the embryo sac is of the *Allium* (bisporic) type (Bawa, 1970).

antipodal cells are usually ephemeral but may multiply to about seven (e.g. in *H. gentianoides* and *H. punctatum)* and persist into early embryogeny. The endosperm is nuclear, although early cell-formation misled some authors into thinking that it was helobial (cf. Stenar, 1938).

The embryogeny in the Hypericoideae, as in *Ploiarum* (Prakash & Lau, 1976), is Solanad (i.e. the terminal cell divides by a transverse wall during the second cell generation and the basal cell forms a several-celled suspensor), whereas in the other subfamilies it is Onagrad (Davis, 1966). Bugnicourt (1971*a*) gives a detailed account of the embryogeny of *H. tetrapterum* (sect. 9. *Hypericum*) and evaluates previous work on the genus.

(*b*) *Abnormalities*

Polyembryony occurs in *Hypericum tetrapterum*, where Bugnicourt (1970, 1971*a*) observed additional embryos formed from a synergid by apogamy and twin embryos produced as buds from the suspensor. Earlier, Noack (1939) reported that in *H. perforatum* aposporous (unreduced) embryo sacs occurred in 97% of the ovules observed, and that these unreduced egg-cells are occasionally fertilised. On the other hand, pseudo-polyembryony resulting from the concrescence of two or more ovules has also been reported in *H. perforatum*, as well as in *H. maculatum* and *H. tetrapterum* (sect. 9. *Hypericum*) and various species in other, distantly related sections (Bugnicourt, 1971*b*).

Germination

(*a*) *The process*

As was shown above (p. 112), the seeds and embryos of the Hypericoideae and Bonnetioideae (at least those of *Ploiarium*) are basically similar, but they differ from those of the other subfamilies of Guttiferae; and similar major differences occur in the germination process. In those taxa with free, developed cotyledons (Hypericoideae, Bonnetioideae, Clusieae), the germination is epigeal, whereas in those taxa where the hypocotyl is swollen and the cotyledons vestigial (Moronobeoideae, Garcinieae) or the cotyledons are enlarged and united (Calophylloideae), the germination is hypogeal (Brandza, 1908). *Clusia* is somewhat intermediate in that the hypocotyl is swollen, but the cotyledons still function.

Brandza (1908), who made a definitive study of seed-structure and germination in the Guttiferae, found that in *Hypericum* (of which he studied numerous species) the emergence of the radicle is followed immediately by the development of a ring of strong root-hairs at the base of the quickly elongating hypocotyl. These hairs appear to serve as an anchor for the developing seedling. They persist for a long time, until after the first foliage leaves have developed.

Brandza's observations agree with those made by other authors (e.g. Ohlendorf (1907) on *H. elodes*), and they have been confirmed many times during this study; but his remark that the radicle always gives rise to the main root, although true, requires some comment. Brandza himself noted that, in *H. perforatum* and *H. elodes*, strong adventitious roots soon develop from the hypocotyl and young stem base; and, indeed, in some sections of *Hypericum* the main root withers or becomes indistinguishable from the adventitious ones. In sects 29. *Brathys* and 30. *Spachium* (and probably also in the whole of the *Hirtella* group, sects 17–19), however, the radicle becomes a taproot, and adventitious roots develop only in species with decumbent or prostrate stems (e.g. *H. scioanum*).

(*b*) *Factors influencing germination*

Experimental studies of germination in *Hypericum* by Kinzel (1913, 1920) showed that most of the seeds would germinate only in light (at 20°C). The species studied were Central European herbs belonging to various sections, and all showed this light requirement except *H. humifusum* in part. Seeds of this species from plants growing in loose arable soils germinated in the dark at 20°C, but seeds from plants of clay soils behaved as obligate light-germinators. Subsequent authors have confirmed the light requirement for *H. perforatum* (Gensini, 1967) and *H. japonicum* (sect. 30. *Spachium*) (Isikawa, 1962).

Vegetative development

As far as I am aware, there have been no studies on the vegetative ontogeny of *Hypericum* other than the paper by Zimmermann (1928) on the vegetative apex in *H. hookeranum* and *H. uralum* (both sect. 3. *Ascyreia*). On the other hand, several investigators have studied the ontogeny of the flower.

Floral development

Although the basic structure of the flower of *Hypericum* is best demonstrated by means of a study of its floral vasculature (see p. 128), the earliest floral studies were ontogenetical; and such studies have continued to be published over the years.

Payer (1857) described the floral whorls in various species as appearing in acropetal succession, with the sepals developing quincuncially (i.e. in 2/5 spiral succession), the petals simultaneously, the androecial primordia shortly afterwards and, very soon after them, the 5–2 members of the gynoecium. In species with a trimerous androecium the double stamen fascicles were seen to have larger primordia than the single one, and in each case the stamens developed in centrifugal succession. In *H. prolificum* (sect. 20. *Myriandra*) the original five primordia soon united in a ring, thus producing the apparently polyandrous state of the mature flower.

Later authors have elaborated or disagreed with Payer's account, but it remains essentially valid. Hofmeister (1868) claimed that the petal primordia appeared after those of the androecium; but Molly (1875), Sachs (1875), Hirmer (1917) and Leins (1964) all agreed with Payer. Sattler (1972) remarks that the interval between the initiation of the whorls, if it exists at all, is so short in *H. perforatum* that it could not be demonstrated with certainty. The difficulty, according to Molly, is that the petal primordia are soon concealed by the fascicle primordia, which develop more quickly.

Breindl (1934), as we have already seen (p. 86), showed that the time and position of origin of the sepals, although basically following a 2/5 spiral succession, were modified by the change from foliar to calycine phyllotaxis.

In *H. elodes* and *H. aegypticum*, Hirmer (1917) described the fasciclodes as arising long after the androecium had been initiated, and Leins (1964) indirectly corroborated his observations. All accounts agree that the stamens arise centrifugally on the fascicle primordium (where one is visible) or directly on the torus, as they do in all closely related families; but Leins (1971) and Sattler (1976) have pointed out that the direction of stamen initiation is not such a fundamental character as it was thought to be by Corner (1946) and Cronquist (1968), for example. Indeed, Cronquist's placing of the Myrtales in the Rosidae appears to be based largely on its having centripetal stamens, whereas most other considerations appear to indicate a relationship with the Guttiferae.

Hirmer, being unable to see five original antipetalous fascicle primordia in *H. prolificum*, suggested that the first groups of three stamens were antisepalous; but Payer's observations are more likely to be correct in view of the structure of the flower of this species as revealed by its vasculature. In any case, Hirmer himself described the first stamen groups of *H. drummondii*, another 'afascicular' species, as antipetalous.

In general, then, the ontogenetic data support those from morphology in indicating a close relationship between the petal and the stamen fascicle interior to it. The relatively late origin of the fasciclodes in *Hypericum* is consistent with the anatomical data (see p. 140) in suggesting that these organs provide an example of 'evolutionary recall' (Robson, 1972*a*).

7. Floral vasculature

Introduction

At an early stage in these studies, it was realised that the vascular structure of the flower could give a clue to the basic floral structure in the Hypericoideae and its variations. Following earlier investigations (van Tieghem, 1875; Henslow, 1890), Saunders (1936, 1939) had laid the foundations of this study in *Hypericum*; but she confined her attentions to species with a fasciculate androecium. Moreover, her observation that the 'hypogynous bodies' of *H. elodes* and *H. aegypticum* were not vascularised (Saunders, 1936) conflicted with that of Hirmer (1917), who saw numerous 'rudimentary' (i.e. vestigial) vascular strands in them. The only reference to other species of Hypericoideae had been made by Wilson (1937), who described part of the floral vasculature of *Vismia dealbata*. The results of this work were presented as part of a thesis (Robson, 1956), and a summary of some aspects of it has been published (Robson, 1972*a*).

Materials and methods

The material was mostly reconstituted from herbarium specimens (Tillson & Bamford, 1938), but some was fresh and was depigmented in 1 : 1 alcohol-acetone. For bleaching, the method described by Vautier (1949) was adopted at first, later being replaced by the use of commercial bleach, which produced quicker results. The buds were cleared in lactic acid (Sporne, 1948).

The species studied were as follows (for details, see Robson [1956]):

HYPERICUM

Sect. 1. *Campylosporus* : *H. revolutum.*
3. *Ascyreia* : *H. oblongifolium*, *H. calycinum*, *H. forrestii.*
5. *Androsaemum* : *H.* x *inodorum.*
7. *Roscyna* : *H. ascyron.*
9. *Hypericum* : *H. erectum*, *H. scouleri*, *H. punctatum.*
9a. *Concinna* : *H. concinnum.*
10. *Olympia* : *H. olympicum.*
14. *Oligostema* : *H. humifusum.*
18. *Taeniocarpium* : *H. pulchrum*, *H. thymifolium.*
20. *Myriandra* : *H. prolificum*, *H. kalmianum*, *H. ellipticum*, *H. crux-andreae* (*H. stans* (Michx.) Adams & Robson), *H. hypericoides.*
21. *Webbia* : *H. canariense.*
25. *Adenotrias* : *H. aegypticum.*
26. *Humifusoideum* : *H. saruwagedicum*, *H. natalense*, *H. peplidifolium.*
27. *Adenosepalum* : *H. aethiopicum* subsp. *sonderi.*
28. *Elodes* : *H. elodes.*
29. *Brathys* : *H. goyanesii.*
30. *Spachium* : *H. brasiliense*, *H. canadense*, *H. gentianoides.*

VISMIA

V. magnoliifolia Cham. & Schlecht., *V. crassa* (Rusby) Blake, *V. guianensis* (Aublet) Choisy, *V. micrantha* Mart.

CRATOXYLUM

C. cochinchinense (Lour.) Blume.

TRIADENUM

T. walteri (J. F. Gmelin) Gleason.

PLOIARIUM

P. alternifolium (Vahl) Melch.

Hypericum—the torus

(*a*) *Basic plan*

The basic plan of the toral vasculature in *Hypericum* is shown as a coplanar diagram in Fig. 32. The sepal traces (S 1–5), which depart from the stele at different levels, are unilacunar but divide into three almost immediately. Above each of them, the lacuna is large, due to the absence of the antisepalous androecial whorl. The petals, likewise, have unilacunar, three-branched traces (P); but they all depart at the same stelar level. Above each one is a relatively massive stamen-fascicle trace (St), also three-branched; and the remaining stelar tissue vascularises the gynoecium, first branching into three to form the dorsal carpel trace (CD)

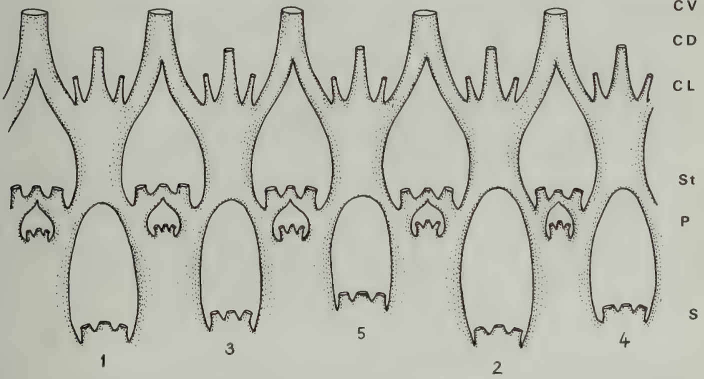


Fig. 32 Basic (primitive?) plan of toral vasculature in *Hypericum*. Legend used in Figs 32–52: CD = dorsal carpel trace; CL = lateral carpel trace; CSL = commissural lateral trace; CV = ventral carpel trace; OC = outline of carpel; OTT = ovule traces; P = petal trace; S_{1-5} = sepal trace (1–5); SL = lateral sepal trace; SM = sepal midrib trace; ST = stamen fascicle trace; Std = fasciclode (i.e. sterile fascicle) trace; VStd = vestigial fasciclode trace.

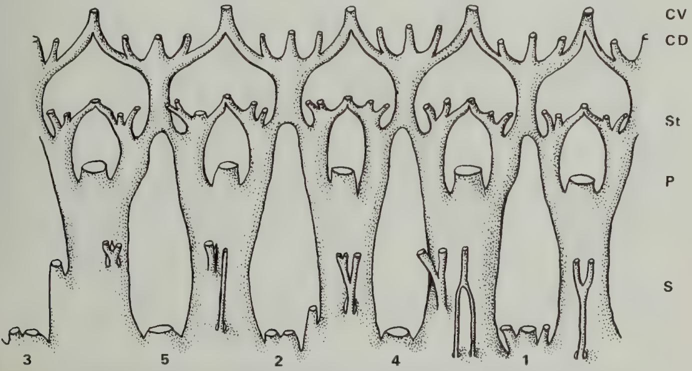


Fig. 33 Plan of toral vasculature of *H. revolutum* (sect. 1) (see Fig. 36a).

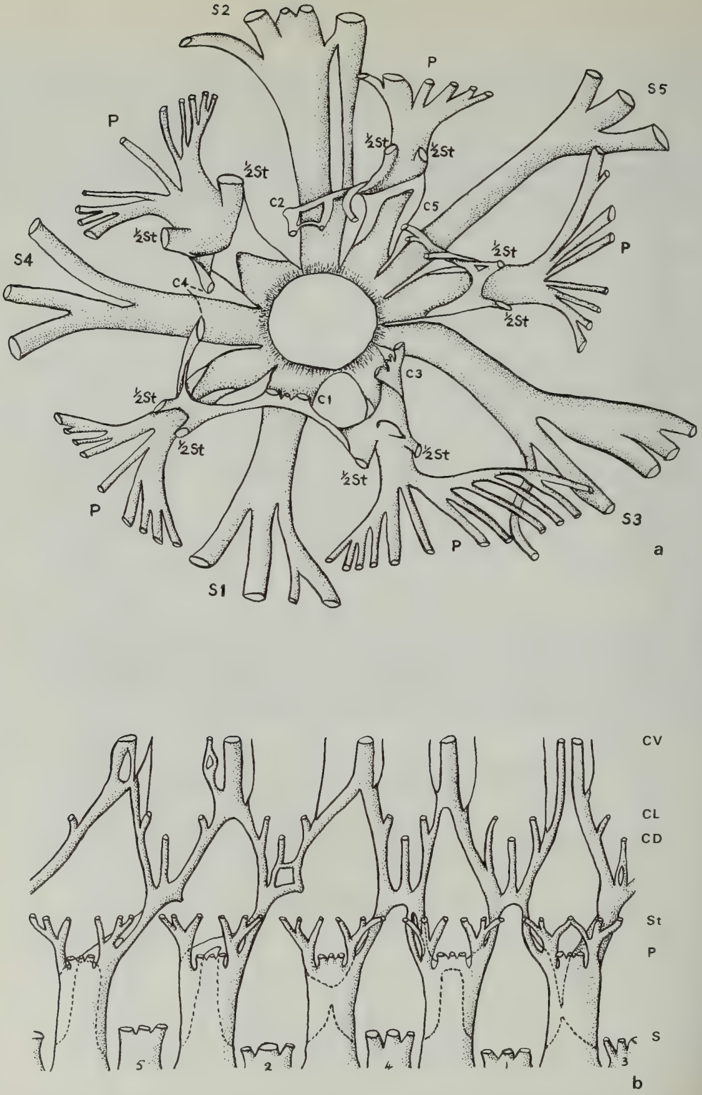

S2
P
S5
½St
½St
P
½St
C2
C5
½St
P
½St
S4
C4
C3
½St
C1
½St
½St
½St
½St
P
P
S3
a
S1
CV
CL
CD
St
P
S
5
2
4
1
3
b

Fig. 34 Toral vasculature of *H. forrestii* (sect. 3): (a) from above (x 25); (b) plan (see Fig. 36b).

and two laterals (CL). The residual tissue comprises five ventral carpel traces (CV), which innervate the placentae and then dichotomise (see Fig. 48).

(*b*) *Isomerous pentamerous flowers*

No flower was found to have all the features of this idealised vascular pattern. *Hypericum revolutum* (sect. 1. *Campylosporus*) very nearly has it (Figs 33, 47a), but the sepal traces are 2–3(4)-lacunar with the laterals partly (S 1–3) or wholly (S 4, 5) commissural. On the other hand, in the flower of *H. forrestii* (sect. 3. *Ascyreia*) depicted in Figs 34 and 47b the sepal traces are all unilacunar; but the upper parts show the results of the developmental strains that were discussed above (p. 86), the greatest distortion being evident near sepal 5. Note also that there is only one true petal-trace lacuna, as four of the stamen-fascicle traces depart as two halves, i.e. without joining to form an arc. Not all regularly pentamerous flowers show such stress effects, however. In *H. ascyron* (Fig. 35), the sepal traces are 3-lacunar with commissural laterals, whereas the stamen-fascicle traces form arcs before departing.

Another trend, namely one of relative vertical condensation, can be seen by comparing the lateral half-stele views of these three species (Fig. 36). This is more pronounced in the flowers of other sections. The other regularly pentamerous flowers (of *H. oblongifolium* and *H. calycinum*) had a vascular structure essentially similar to those already described.

(*c*) *Flowers with pentamerous androecium and trimerous gynoecium*

Where the gynoecium has become trimerous, as in *Hypericum* x *inodorum* (Fig. 37), the elimination of two carpels is not completely reflected in the vascular structure. The dorsal traces of carpel 1 are only slightly distorted, but those of the other two are both compound, including parts of the traces to the 'missing' carpels 4 and 5. It is clear, however, that the contractions have occurred along the radii of sepals 4 and 5.

(*d*) *Flowers with trimerous androecium and gynoecium*

In a large-flowered species with trimerous inner whorls (e.g. *Hypericum olympicum*, Figs 38, 47d), all signs of carpels 4 and 5 are absent; but all five androecial traces are still present, one single (above petal 1/3) and the others in pairs (above sepals 4 and 5). The morphological evidence of union of fascicles, discussed above (p. 100), is thus reflected in the traces to these

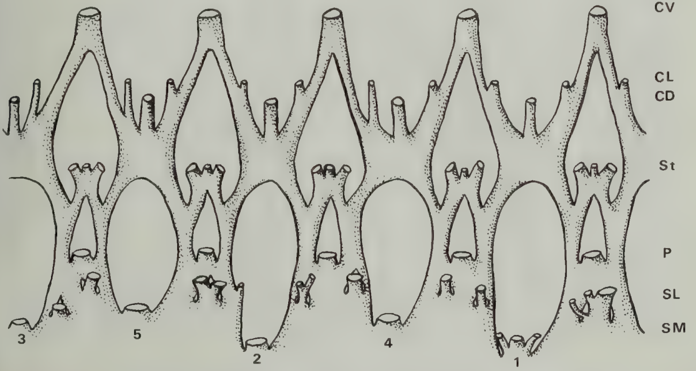


Fig. 35 Plan of toral vasculature of *H. ascyron* (sect. 7) (see Fig. 36c). Note that stamen-fascicle traces are single (in fact, curved) for some distance.

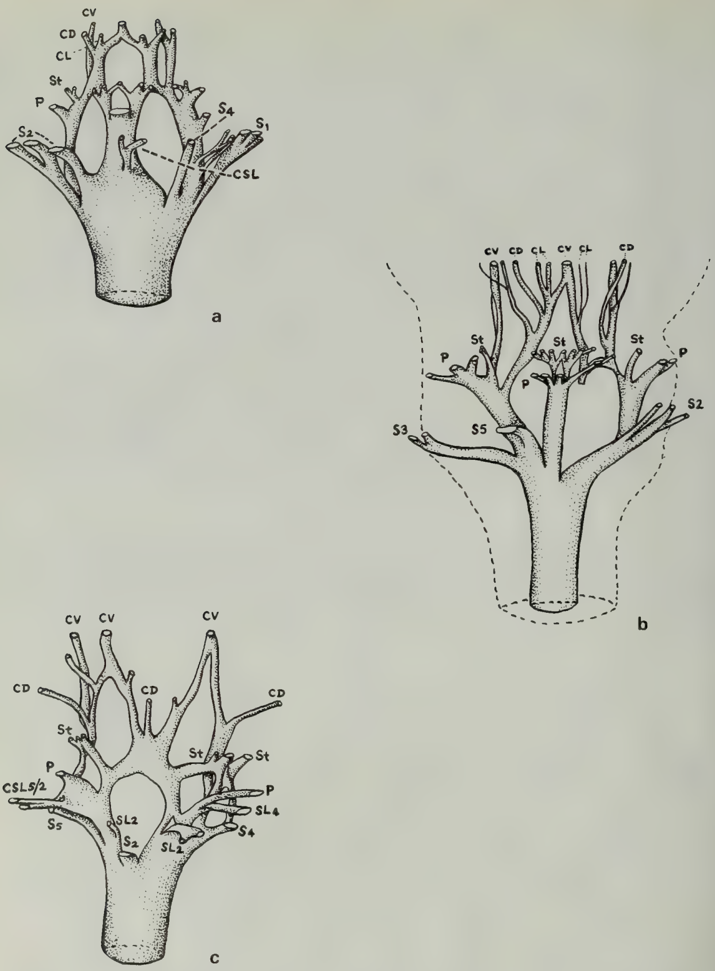

CV
CD
CL
St
P
S2
S4
S1
CSL
a
CV
CD
CL
CV
CL
CD
St
St
St
P
P
P
S3
S5
S2
b
CV
CV
CV
CD
CD
CD
St
St
St
P
P
CSL5/2
S5
SL2
S2
SL2
SL4
S4
c

Fig. 36 Half toral vasculature of: (a) *H. revolutum*; (b) *H. forrestii*; (c) *H. ascyron* (all x 20).

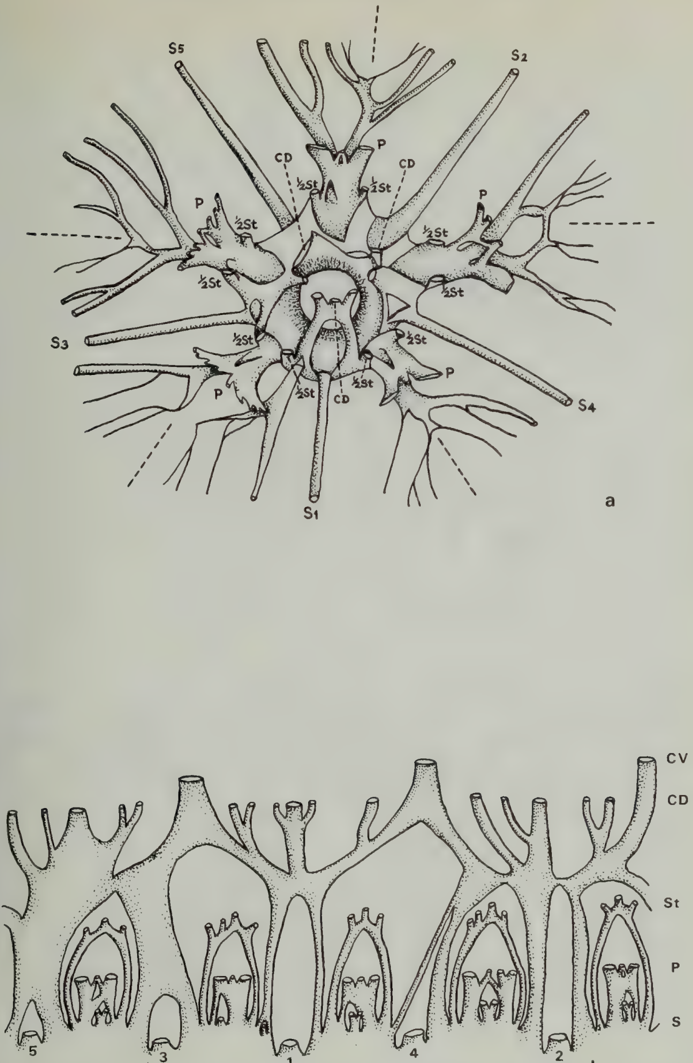

S5
S2
P
CD
½St
CD
½St
P
½St
½St
½St
½St
S3
½St
½St
P
P
½St
CD
½St
S4
S1
a
CV
CD
St
P
S
5
3
1
4
2
b

Fig. 37 Toral vasculature of *H.* x *inodorum* (sect. 5): (a) from above (x 15); (b) plan.

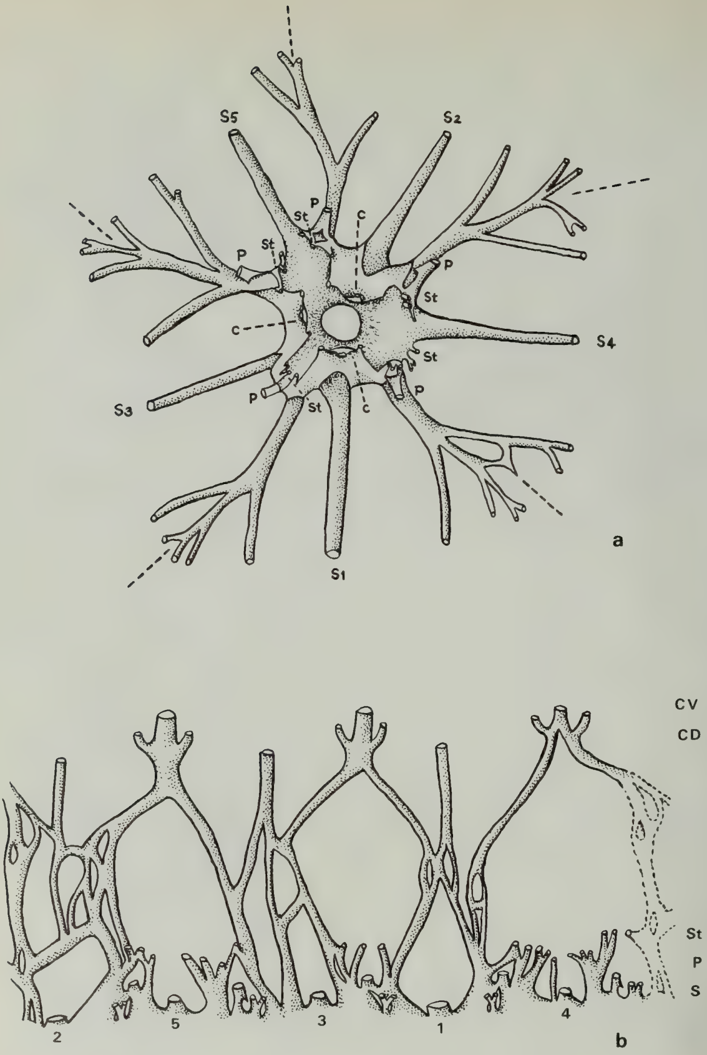

S5
S2
P
St
c
S4
S3
S1
a
CV
CD
St
P
S
2
5
3
1
4
b

Fig. 38 Toral vasculature of *H. olympicum* (sect. 10): (a) from above (x 20); (b) plan. Note the merging of stamen-fascicle traces 2/4 and 3/5.

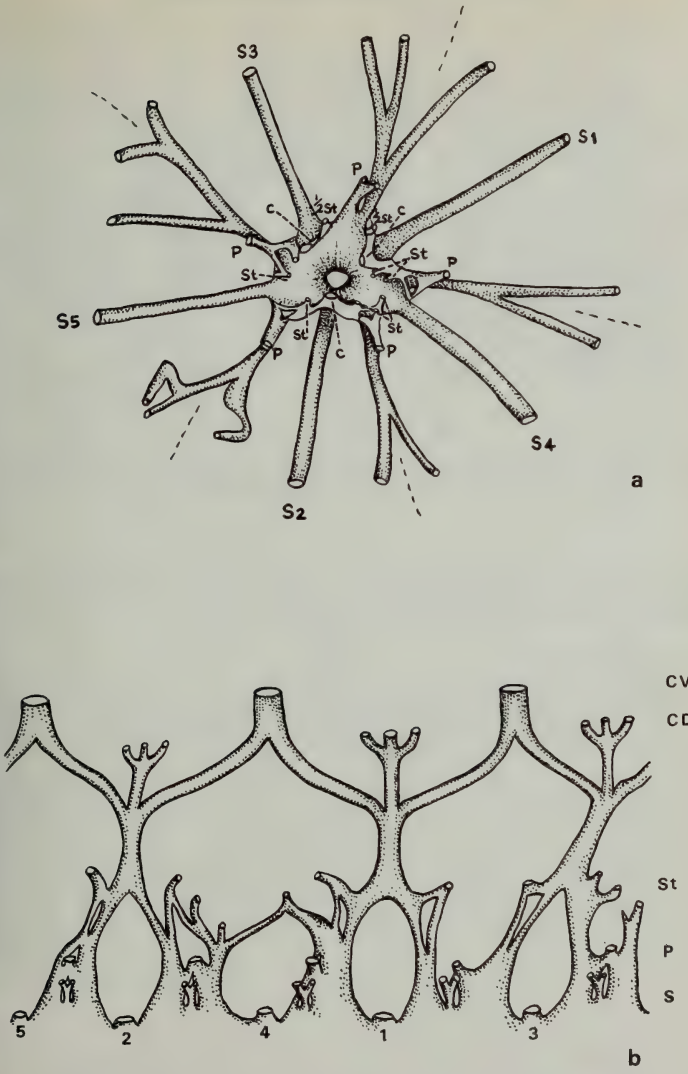

S3
S1
P
½St
C
½St
C
P
St
P
St
S5
St
C
St
P
P
S4
a
S2
CV
CD
St
P
S
5
2
4
1
3
b

Fig. 39 Toral vasculature of *H. pulchrum* (sect. 18): (a) from above (x 36); (b) plan.

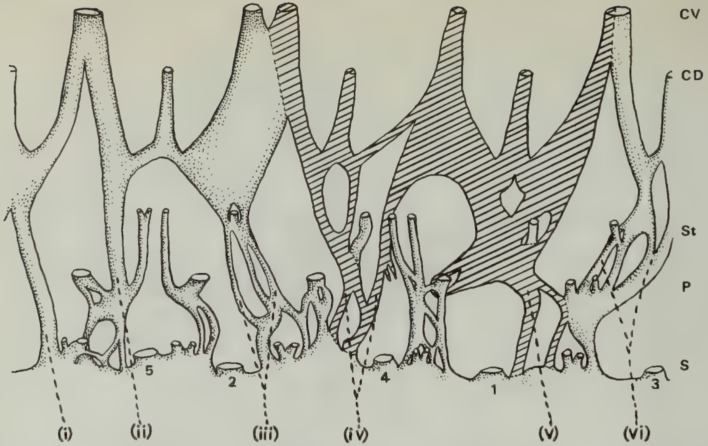


Fig. 40 Plan of toral vasculature of a 4-carpellary flower of *H. natalense* (sect. 26), showing that the trace to carpel 4 is derived from that of carpel 1 of a 3-carpellary gynoecium.

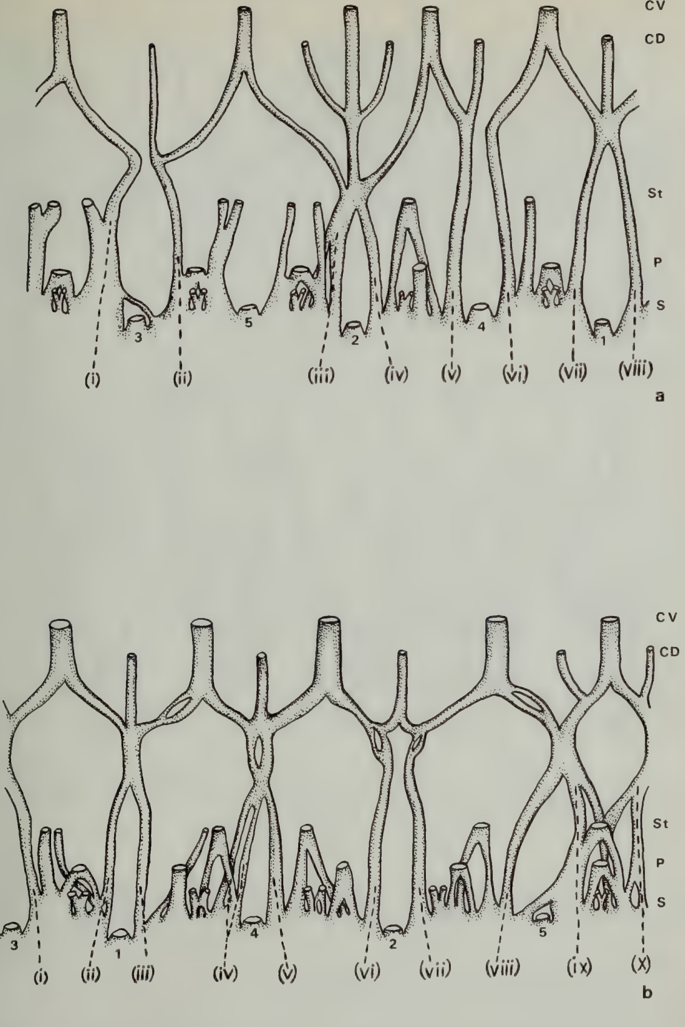
organs. In smaller-flowered species (*H. pulchrum* (Figs 39, 47e) and *H. aethiopicum* subsp. *sonderi*), the vascular plan is essentially similar but simpler, as it is in the species with fasciclodes, *H. aegypticum* and *H. elodes* (Robson, 1972*a* : figs 8, 9).

(*e*) *Sect.* Humifusoideum

Saunders (1937) investigated *Hypericum peplidifolium* because it was alleged to have three fascicles and five styles (Keller, 1925), which seemed to go against the trend of meiomery starting in the innermost organ. She claimed that all the flowers that she examined had five fascicles, not three; but Milne-Redhead (1953) described this species as having stamens 'usually in 3 often rather indefinite groups of 7–10, but sometimes totalling as many as 10'. *H. peplidifolium* is a relatively advanced, herbaceous member of sect. 26. *Humifusoideum.* When a more primitive, shrubby member (*H. saruwagedicum*) was studied, its toral vasculature was found to be essentially similar to that of *H. goyanesii* (see below, Fig. 45), i.e. with five distinct fascicle traces 'spread out' so that their branches form a more-or-less continuous row. This pattern reflects that of the stamens, which are 'irregular' or 'not in fascicles'. The gynoecium is trimerous.

H. natalense is intermediate between *H. saruwagedicum* and *H. peplidifolium* in having, for example, a 4–5-carpellary gynoecium and stamens 'irregularly arranged in 3 or 4 indistinct groups' (Killick & Robson, 1976). Figure 40 shows that the grouping of the androecial traces is also indistinct, and that the fourth carpel is innervated by the division of the trace opposite sepal 1 (shaded area) of a 3-carpellary gynoecium.

In *H. peplidifolium* (Fig. 41) this doubling process has been repeated opposite sepal 2 (Fig. 41a) or 3 (Fig. 41b); and the androecial traces reflect the restored pentamery to a greater (Fig. 41a) or lesser (Fig. 41b) degree. The vascular pattern of the torus therefore supports the hypothesis, based on gross morphological trends, that the androecium and gynoecium in sect. 26. *Humifusoideum* is secondarily pentamerous.


CV
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St
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(i)
(ii)
(iii)
(iv)
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(viii)
a
CV
CD
St
P
S
3
1
4
2
5
(i)
(ii)
(iii)
(iv)
(v)
(vi)
(vii)
(viii)
(ix)
(x)
b

Fig. 41 Plans of toral vasculature of 5-carpellary flowers of *H. peplidifolium* (sect. 26), showing: (a) irregular stamen-fascicle traces, with traces to carpel 5 derived from those to carpel 2; more regular stamen-fascicle traces, with traces to carpel 5 derived from those to carpel 3. (i)-(x) = half carpel-traces (numbered from l. to r., i.e. numbers in (a) and (b) do not correspond).

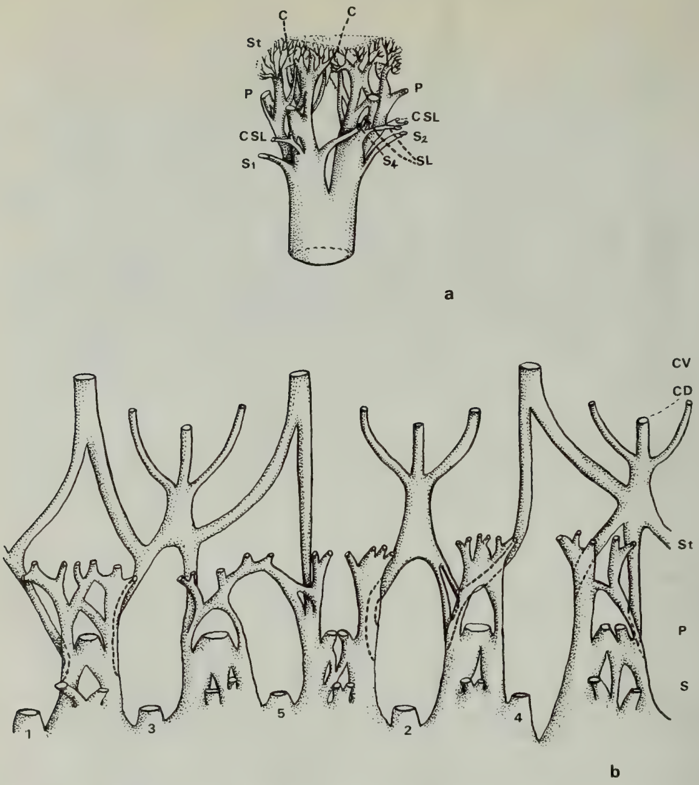

Fig. 42. Toral vasculature of *H. prolificum* (sect. 20): (a) half (lateral view) (x 28); (b) plan. Note the union of stamen-fascicle traces on either side of sepal 5.

(f) Polyandrous species

Keller (1925) described three sections of *Hypericum* as having polyandrous afasciculate androecia, viz. *Campylopus*, *Myriandra* and *Brathys*. Of these, sect. 11. *Campylopus* (i.e. *H. cerastoides*) was found to have five fascicles of stamens which varied from free to united 1 + 2 + 2; and, as the fascicles were all only slightly united at the base, they were easily separable; sect. 20. *Myriandra* now includes the 'genus' *Ascyrum* L.; and *Brathys* has proved to comprise two independent sections, 29. *Brathys* and 30. *Spachium* (Robson, 1977*a*).

In sect. *Myriandra* the stamens are inserted on a relatively wide toral zone and are shed individually, and the androecial traces are likewise branched to cover a wide area (Figs 42, 47g). These traces, however, are basically similar to those of fascicled species (Figs 33–39), except that there is greater lateral condensation and less vertical condensation. Continued lateral condensation is correlated with meiomery of the perianth in the species formerly

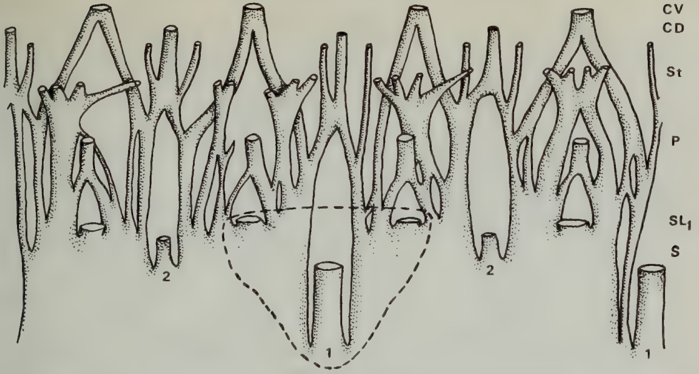

Fig. 43 Plan of toral vasculature of *H. crux-andreae* (sect. 20).

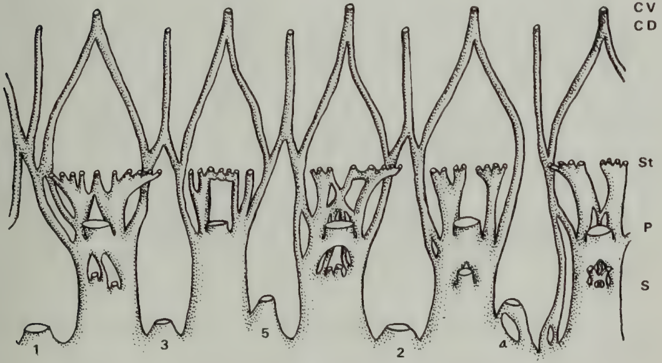

Fig. 44 Plan of toral vasculature of *H. brasiliense* (sect. 30).

placed in *Ascyrum*; but, here too, the fascicle traces are visible. They have, of course, been reduced in number to four (Fig 43, 47h).

In sects 29. *Brathys* and 30. *Spachium*, on the other hand, the androecial zone is relatively narrow, the stamens often forming only a single row. Even so, the basic toral vasculature is typical (Figs 44, 45), with five fascicle traces clearly visible. In those species of sect. *Spachium* where the flowers are smaller and the stamens fewer, e.g. *H. canadense* (Figs 46, 47k), the discontinuous ring of stamens is reflected in a less regular vascular pattern; but the five fascicle traces are still present. The whole flower, however, has undergone relative vertical condensation in these sections, so that the stamens can be said to have been 'squeezed out' into a narrow ring.

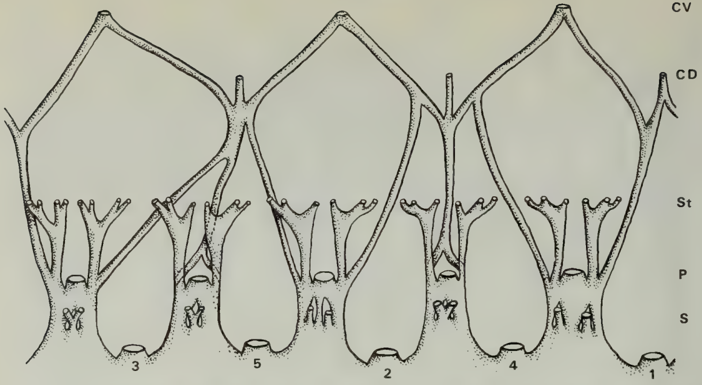

Fig. 45 Plan of toral vasculature of *H. goyanesii* (sect. 29). Note how five carpel traces serve three carpels (1, 2 + 4, 3 + 5).

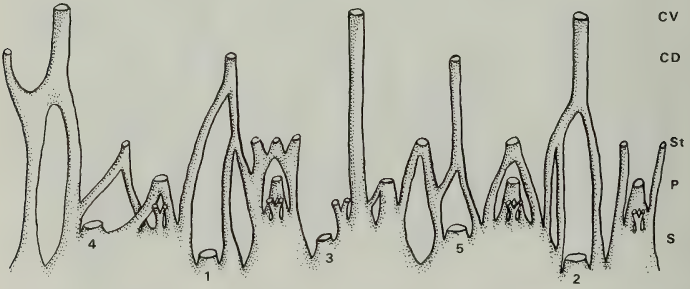

Fig. 46 Plan of toral vasculature of *H. canadense* (sect. 30). Note the extreme 'dissection' of the carpel traces.

(*g*) *The 'Elodes' group*

Hypericum aegypticum and *H. elodes* have toral vasculature that is typical of '3 + 3' *Hypericum* species. The fasciclodes have no vascular connections with the stele (cf. Robson, 1972 : figs 8, 9). In *H. aegypticum* but not *H. elodes*, however, there are obscure vestigial vascular strands within the fasciclode.

***Hypericum*—the ovary**

Species of *Hypericum* with large ovaries have a dorsal carpel trace that branches in the ovary wall and near the stigma, and the lateral carpel traces penetrate to the style and dichotomise (Fig. 48a). In more advanced species with a relatively massive style, the branching of the dorsal trace may begin at a lower level (Fig. 48b); but the general trends are towards reduction of the branching and elimination of the lateral traces (Fig. 48c, d).

Other genera

In contrast to the fasciclodes of the 'Elodes' group, those of *Ploiarium*, *Vismia*, *Cratoxylum* and *Triadenum* are fully vascularised (cf. Robson, 1972*a* : figs 5–7; Baas, 1970), their traces bearing the same relationship to those of the sepals as the stamen fascicle traces bear to those of the petals. This relationship is clear in the regularly pentamerous *Vismia* (Fig. 49) (cf. also Wilson (1937 : fig. 29)); and even in *Cratoxylum*, where the androecium and gynoecium are trimerous, there are vestigial traces to the two 'missing' fasciclodes (Fig. 50). The traces to the stamen fascicles opposite the sepals, however, are double in this genus and in *Triadenum* (Fig. 51), as they are in *Hypericum*. The ovary vasculature of *Vismia* and *Cratoxylum* is more complex than in *Hypericum*, (i) being more elaborately branched and (ii) having the lateral carpel traces always departing from the dorsal carpel trace (Fig. 52a, b). *Triadenum* shows a simplification of the *Cratoxylum* pattern (Fig. 52c).

Discussion

From the vascular patterns described above, it will be seen that the floral anatomy of *Hypericum* can be interpreted in terms of variations on a basic plan (Fig. 32). These variations in general parallel the morphological changes already discussed (e.g. the formation of 'double' stamen fascicles) and frequently indicate a previous evolutionary stage when gross-morphological evidence for this has disappeared (e.g. the 5- or 4-fascicled nature of the androecium in sect. 20. *Myriandra*).

The patterns in *Vismia* and *Ploiarium* (not illustrated, but essentially similar to that of *Vismia*) support the idea that these genera have isomerous pentamerous diplostemonous androecia (i.e. that the fascicle functions as the androecial unit), and that the androecium becomes haplostemonous in *Hypericum* by suppression of the antisepalous whorl. The floral vascular pattern also allows discrimination between meiomery resulting from the loss of an organ (e.g. the perianth members of tetramerous *Hypericum* species or the gynoecium of *Cratoxylum*, *Triadenum* and some species of *Hypericum*) and from fusion of adjacent organs (e.g. the androecia of *Cratoxylum*, *Triadenum* and some species of *Hypericum*). Finally, the relationship of the fascicle or fasciclode trace to that of the sepal or petal below it is comparable with the trace of an axillary branch to that of its subtending leaf, thus lending support to the Gonophyll Theory (Melville, 1962, 1963).

Likewise, the alternation of dorsal or dorsal-plus-lateral carpel traces (supplying the 'carpel' wall and style) with ventral carpel traces to the placenta and ovules invites comparison with the alternation of sepal and petal traces. In other words, the traces to the 'carpel' walls and the placentas remain independent. There is therefore no vascular evidence in *Hypericum* and related genera that favours the Carpel Theory—*pace* Dupuy & Guédès (1975). Indeed, it seems to be special pleading to interpret the strong vasculature of the *Hypericum* placenta as related to its nutritive function alone. 'Occam's Razor' would require one to describe the ovary of *Hypericum* species with a pentamerous gynoecium as comprising five foliar organs on the sepal radii alternating with five, usually 2-lobed placentae on the petal/stamen-fascicle radii (see p. 106 and Figs 23, 24). In terms of the Gonophyll Theory these are five tegophylls alternating with five fertile gynophyll branches. The two components usually become separated in fruit, the tegophylls being easily removable, leaving the five or fewer 2-lobed placental branches as a 1–5-partite 'column'.

The evidence from floral vasculature has a bearing on two more morpho-evolutionary controversies:

(i) The behaviour of the stamen fascicle and fasciclode as androecial entities (i.e. as equivalent to a single stamen and staminode in oligostaminal flowers) indicates that the individual stamens in each fascicle are to be interpreted as branches of this entity. Increase or decrease in stamen number and direction of maturation are thus equivalent to a variation in the amount of branching, not to an increase or decrease in numbers of whole organs. They are not, therefore, of fundamental evolutionary significance; and it would seem to be wrong

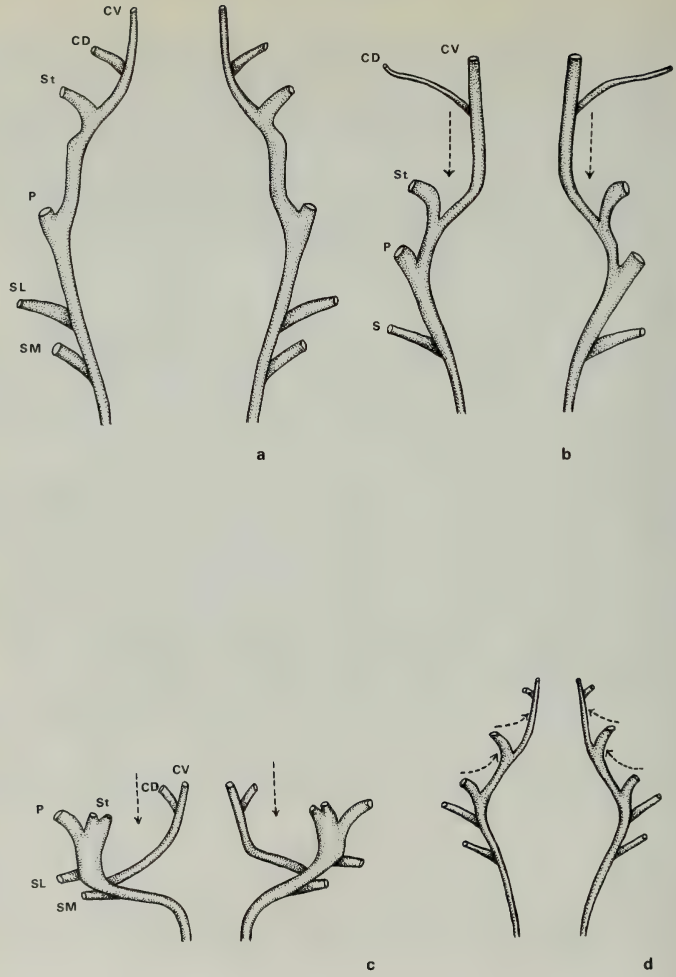
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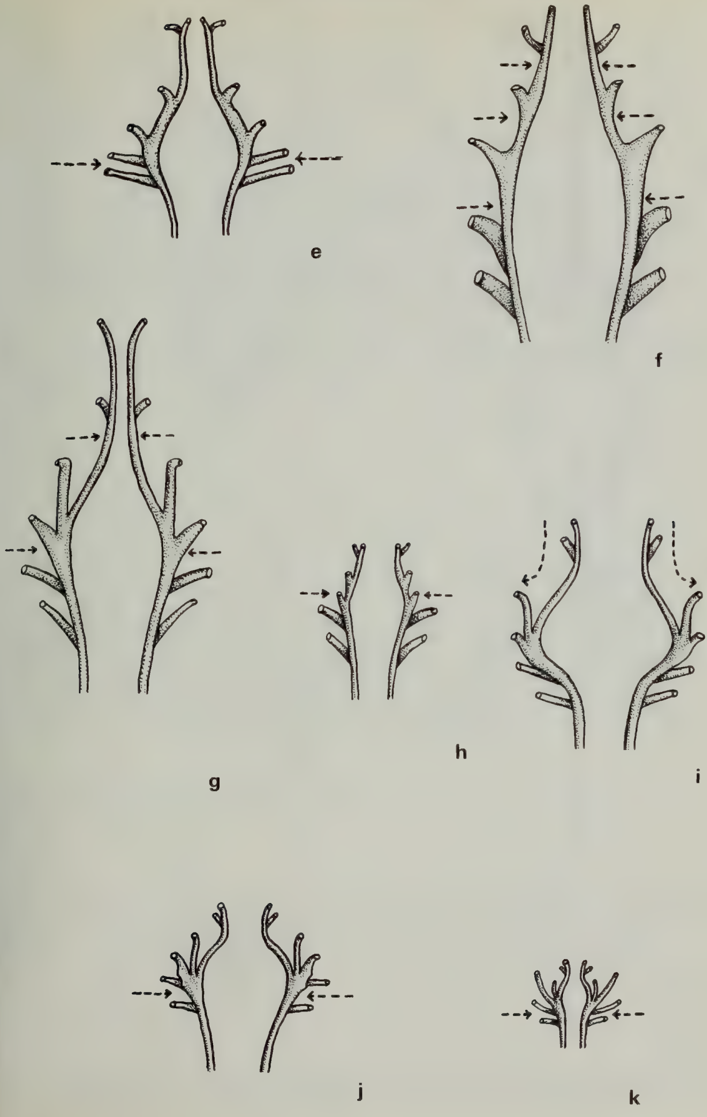
Fig. 47 Longitudinal sections of toral vasculature of *Hypericum* species, showing some trends in vertical and lateral condensation (numbers indicate sections): (a) *H. revolutum* (1); (b) *H. forrestii* (3); (c) *H. calycinum* (3); (d) *H. olympicum* (10); (e) *H. pulchrum* (18); (f) *H. canariense* (21); (g) *H. prolificum* (20); (h) *H. hypericoides* (20); (i) *H. goyanesii* (29); (j) *H. brasiliense* (30); (k) *H. canadense* (30) (a–d × 23, e–k × 28).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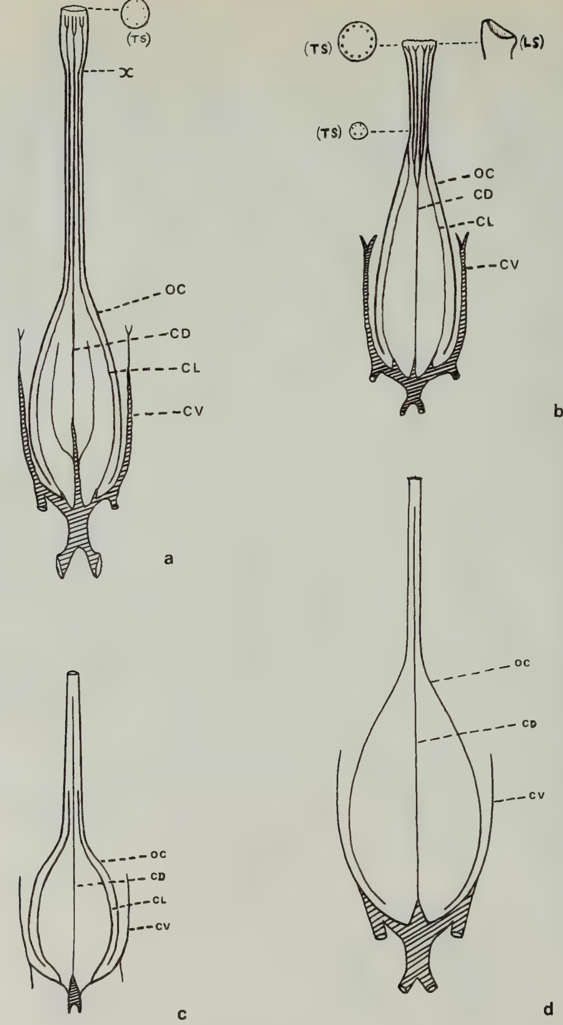
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Fig. 48 Carpel vasculature in *Hypericum* (omitting ovule traces): (a) *H. revolutum* (x c. 10); (b) *H. ascyron* (x c. 12); (c) *H. olympicum* (x 14); (d) *H. aethiopicum* subsp. *sonderi* (x c. 12).

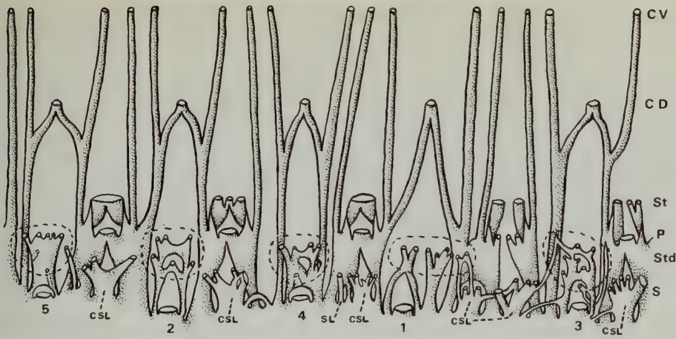

Fig. 49 Plan of toral vasculature of *Vismia guianensis*, showing that the fasciclode traces (Std) bear the same relationship to the sepal traces as the stamen-fascicle traces (St) do to the petal traces.

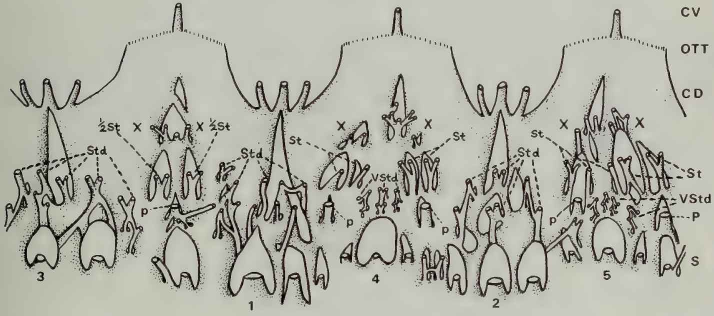

Fig. 50 Plan of toral vasculature of *Cratoxylum cochinchinense*, showing two vestigial fasciclode traces (V Std). X = 'blind' stamen-fascicle traces.

to apply the term 'centrifugal' to both the direction of maturation of stamens in a fascicle and obdiplostemony (Sattler, 1976; Tucker, 1976). The latter is a function of the relative time of maturation of whole organs, not branches. For example, the delayed development of the fasciclodes in *Hypericum aegypticum* and *H. elodes* results in this condition.

(ii) Union of stamen fascicles and union of stamens within a fascicle are equivalent to the union, respectively, of organs and branches of organs. The two trends are distinct, though frequently concurrent. It is doubtful if any member of the Guttiferae retains any of the primitive 'trunk' of the stamen fascicle very far above the toral level (see p. 99). In every case examined, e.g. *Hypericum aegypticum* and *H. elodes* (Robson, 1956), the Moronobeoideae (Wilson, 1937; Kawano, 1965), *Cratoxylum* (Baas, 1970) and *Garcinia* species (Stebbins, 1974), the traces to the individual stamens run separately through the 'trunk'.

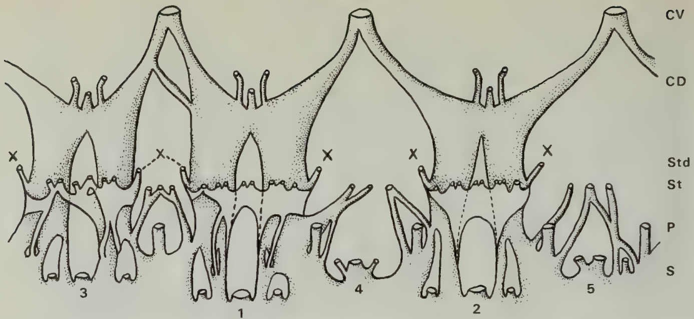

Fig. 51 Plan of toral vasculature of *Triadenum walteri*. Traces marked 'x' serve stamen fascicles, not fasciclodes.

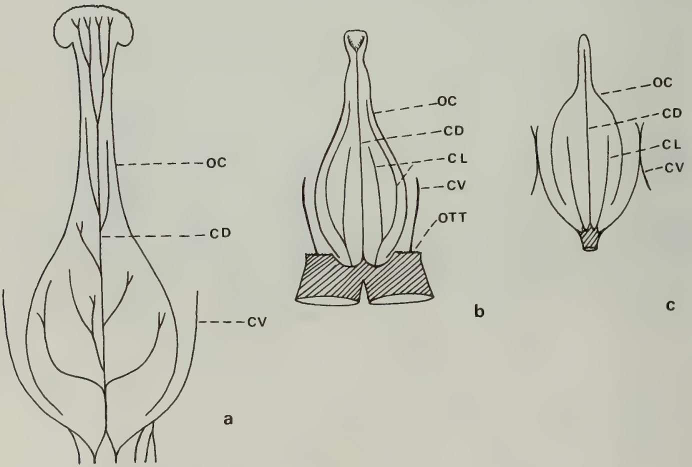

Fig. 52 Carpel vasculature in: (a) *Vismia guianensis* (x 15); (b) *Cratoxylum cochinchinense* (x 9); (c) *Triadenum walteri* (x 9).

8. Anatomy and phytochemistry—taxonomic implications

Vegetative anatomy

The vegetative anatomy of *Hypericum* has been studied by various workers, and summaries and discussions of their conclusions have been published by Vestal (1938) and Metcalfe & Chalk (1950). In addition, Schofield (1968) made a survey of nodal and petiolar anatomy in the Guttiferae and related families. More recently, Baretta-Kuipers (1976) has compared the wood anatomy of Hypericoid genera with that of the rest of the Guttiferae, particularly the Bonnetioideae. In the light of these studies, and because Dr A. C. Gibson (of the University of Arizona, Tucson) is engaged on a comparative anatomical study of the Cratoxyleae and Hypericeae, it is unnecessary to make a further detailed analysis of *Hypericum* anatomy here.

In general, *Hypericum* is anatomically distinct from the genera of Vismieae and Cratoxyleae. Vestal (1938), on anatomical grounds, supported Hochreutiner's (1919) suggestion that it is more closely related to the Clusioideae, but that 'the arborescent Hypericaceae' are derived from the Calophylloideae. This is too simplistic a view; and to link these latter groups through *Psorospermum*, as Hochreutiner and Vestal suggested, is clearly erroneous. Nevertheless, Hochreutiner's proposals serve to emphasise the distinctness of each of the Hypericoid tribes. Baretta-Kuipers (1976) states that these tribes 'are all quite different [in wood anatomy] from the Bonnetiaceae', but the data in her table 2 do not seem to bear this out. From a relatively cursory study of the literature, I would suggest that the Hypericoideae are anatomically more similar to the Bonnetioideae than they are to other subfamilies of the Guttiferae, but that they are in general most advanced than are the Bonnetioids.

Secretory system

(*a*) *Introduction*

The nature and external distribution of the glands in *Hypericum* have been considered under *Morphology*. It is necessary here to discuss their internal distribution, their chemical composition and their taxonomic significance.

(*b*) *Distribution of secretory cavities and canals*

Secretory canals, containing essential oils, are present in *Hypericum* in the stem and root. They also penetrate, as we have seen, into the leaves, sepals and petals, where (i) they are frequently dissected into streaks and dots (isodiametric lacunae) and (ii) their contents are often denser and darker in colour (Coutinho, 1950; Mathis, 1963). Lastly, they occur in the ovary wall, where they may also become streaks or dots (i.e. vesicles). The external stem glands (when present) and the anther-connective glands are always punctiform or short, and their contents are resinous or waxy.

In the vegetative parts of the plant, the glandular canals are distributed in the following way:

Root — phloem, pericycle.
Stem — medulla (occasionally one central canal, e.g. in *H. calycinum*, *H. balearicum*, *H. linarifolium*), phloem, pericycle, cortex (rarely, e.g. in *H. calycinum*).
Leaf — mesophyll (often dissected), vascular bundles (phloem).

The above data were obtained from Kexel (1896), Costa (1904) and Coutinho (1950). The secretory canals of the Cratoxyleae have a similar distribution, but seem to occur constantly in the stem medulla and possibly the cortex (Kexel, 1896; Holm, 1903; Baas, 1970).

(*c*) *Composition of contents of secretory cavities and canals*

According to Mathis (1963), the essential oils in the secretory tissues of *Hypericum* can be divided into two fractions, volatile and heavy, depending on their behaviour in chemical analysis. The volatile fraction, which contains saturated hydrocarbons and monoterpenes, comprises 60–80% of all the essential oils; and the heavy fraction contains mainly sesquiterpenes, monoterpene alcohols and linear-chain aldehydes. Mathis found that the shrubby species (in sects 3. *Ascyreia*, 5. *Androsaemum*, 6. *Inodora* and 20. *Myriandra*) were rich in (volatile) limonene and often in myrcene, and that there was sometimes a predominance of monoterpene alcohols in the heavy fraction (cf. also Mathis & Ourisson, 1964*a*, *b*). On the other hand, the dwarf shrubs and herbs (in sects 7. *Roscyna*, 9. *Hypericum*, 10. *Olympia*,

Table 6 Distribution of hypericin and pseudo-hypericin in *Hypericum* (modified from Mathis (1963))

Section	Species tested	(No.)	Stem	Leaf	Sepal	Petal	Notes
1. Campylosporus	all	(5)	—	+	+	+	
2. Psorophytum	all	(1)	—	—	—	—	
3. Ascyreia	all	(12)	—	—	—	—	
4. Takasagoya	all	(1)	—	—	—	—	
5. Androsaemum	all	(4)	—	—	—	—	
6. Inodora	all	(1)	—	—	—	—	(*a*)
7. Roscyna	all	(2)	—	—	—	—	
8. Bupleuroides	all	(1)	—	—	+	+	
9. Hypericum	most	(15)	—	+	+	+	
	others	(9)	+	+	+	+	(*b*)
10. Olympia	all	(2)	—	+	+	+	
11. Campylopus	all	(1)	—	+	+	+	
12. Origanifolia	all	(2)	+	+	+	+	
13. Drosocarpium	all	(10)	—	+	+	+	
14. Oligostema	all	(6)	—	+	+	+	
15. Thasia	all	(1)	—	+	+	+	
16. Crossophyllum	*H. orientale*		—	—	—	—	(*c*)
	H. adenotrichum		—	+	+	+	
17. Hirtella	most	(10)	—	—	+	+	(*d*)
	others	(7)	—	+	+	+	
	H. retusum		+	+	+	+	
18. Taeniocarpium	all	(12)	—	—	+	+	(*e*)
19. Coridium	most	(3)	—	—	+	—	
	H. roberti		—	—	+	+	(*f*)
20. Myriandra	all	(16)	—	—	—	—	
21. Webbia	all	(1)	—	—	—	—	
22. Arthrophyllum	all	(3)	—	—	—	—	(*g*)
23. Triadenioides	*H. scopulorum*		—	—	+	+	
	H. pallens		—	+	+	+	
24. Heterophylla	—						
25. Adenotrias	all	(2)	—	—	—	—	
26. Humifusoideum	all	(1)	—	+	+	+	
27. Adenosepalum	most	(16)	—	+	+	+	
	H. aethiopicum		+	+	+	+	(*h*)
28. Elodes	all	(1)	—	—	—	—	(*i*)
29. Brathys	all	(11)	—	—	—	—	
30. Spachium	all	(33)	—	—	—	—	

NOTES: (*a*) *H. xylosteifolium* has two forms, respectively without and with glandular-marginal sepals. Mathis cites a positive record by R. Salgues, which could be from the glandular form. (*b*) All positive records for hypericin in the stem, except that for *H. punctatum* Lam., come from species in the *H. perforatum* group. The failure of Mathis to record them in *H. corsicum* Steudel (= *H. tetrapterum*) may be due to a misidentification. (*c*) Of the two species in this section, *H. orientale* has only amber glands and *H. adenotrichum* has black glands. (*d*) The ten species include three (*H. amanum* Boiss. = *H. amblysepalum*, *H. leptocladum* Boiss. = *H. helianthemoides*, *H. assyriacum* Boiss. = *H. hirtellum* var.) in which presence in the leaves is listed as doubtful. (*e*) *H. fragile*, which is stated to have hypericin in the leaves, belongs to this section; but cultivated material thus named is nearly always *H. olympicum* (sect. 10. *Olympia*). (*f*) *H. roberti* is a synonym of *H. ericoides*, in which the petal margins vary from eglandular to black-glandular. (*g*) *H. rupestre* has glandular-margined sepals but apparently gave a negative result. (*h*) *H. aethiopicum* subsp. *sonderi* (Bredell) N. Robson has a black-glandular stem; in the other subspecies, and in the other species listed, it is eglandular. (*i*) The red marginal glands of the sepals apparently do not contain enough hypericin to give a positive result.

13. *Drosocarpium*, 18. *Taeniocarpium*, 19. *Coridium* and 27. *Adenosepalum*) were poor in limonene and myrcene, and the heavy fraction from them consisted mainly of sesquiterpenes and sometimes of saturated linear-chain aldehydes (cf. also Mathis & Ourisson, 1964*c*, *d*).

On the basis of Mathis's data, it does not seem possible to make any taxonomically more useful generalisations. He found quantitative seasonal variation, as well as variation with age. Thus the volatile fraction is most abundant (i) at the time of flowering (except in *H. calycinum*, where the fruits are particularly rich in volatile substances) and (ii) in young plants (and presumably young parts of plants). The viscosity of the essential oils was 2–10 times as great in the leaves as in the flowers and fruits; and the viscosity of the leaf extract was yellowish, whereas that of the flowers and fruits was almost colourless. The chemical composition of the essential oils in the different parts, however, scarcely varied.

(*d*) *Distribution of hypericin and pseudo-hypericin*

This topic has already been discussed on the basis of presence or absence of dark glands (Fig. 12, p. 82). Mathis & Ourisson (1963) and Mathis (1963) gave the results of a comprehensive investigation of the distribution of these substances, both within the plant and throughout the genus. Their results were expressed in terms of Keller's classification and included references to previously published results. Where these differ from the results of Mathis, they would appear to be due, in most cases, to misidentification or faulty technique. I have not therefore taken these aberrant records into account in Table 6, except in note (*a*).

Table 6, in which Mathis's results have been listed according to my classification (Robson, 1977*a*), should be compared with Fig. 12. It will be seen that the occurrence of black glands in an organ is an accurate indication of the presence of hypericin (and probably pseudo-hypericin) in that organ, but that, if the glands are red (as in the sepals of *H. elodes*), the substances may not be detectable by the methods adopted.

It should also be noted that Mathis did not test *Hypericum* ovaries, some of which also contain black glands, e.g. that of *H. richeri* (sect. 13. *Drosocarpium*).

(*e*) *Chemistry of hypericin and pseudo-hypericin*

Hypericin and pseudo-hypericin, which are naphtho-dianthrones related to emodin, have been recorded only from the Hypericeae. It is not known whether the contents of the dark glands in the Vismieae and Cratoxyleae are chemically identical or not; but the bark of *Harungana madagascariensis* Lam. ex Poiret (Vismieae) was found to contain a related substance, harunganin, which, like hypericin and pseudo-hypericin, has a molecule with the anthranol type of structure (Stout *et al.*, 1962). The molecules of hypericin and pseudo-hypericin are very similar, differing only in one radicle (Fig. 53).

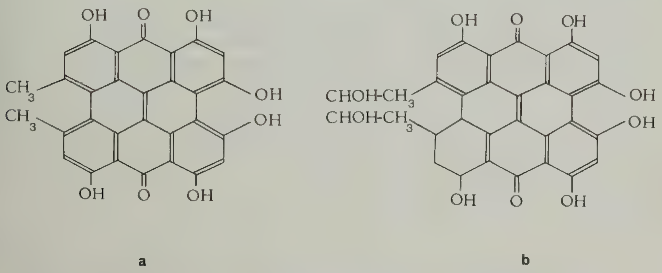

Fig. 53 Molecular structure of: (a) hypericin; (b) pseudo-hypericin (after Mathis, 1963).

Chemotaxonomy of the Hypericoideae

A short summary of chemotaxonomical data on the Hypericoideae, most of which refers to *Hypericum*, was given by Hegnauer (in Robson, 1974). As yet, none of it is relevant to the infrageneric classification of *Hypericum*. The presence of xanthones, however, links the Hypericoideae to the rest of the Guttiferae, including the Bonnetioideae, and differentiates the family from the Theaceae (cf. Kubitzki, Mesquita & Gottlieb, 1978; Gunatilaka, Balusubramian & Kumar, 1979).

Webb (1980), who studied the flavonols and flavonoids in the leaves of the eastern North American species of sect. 30. *Spachium*, found that each of the eleven species had a distinctive chromatographic profile and a characteristic set of compounds.

9. Cytology and genetics

Chromosomes of *Hypericum*

(*a*) *Chromosome numbers*

In a previous paper (Robson & Adams, 1968), a summary was given of the information then available about the chromosome numbers in *Hypericum* and other genera of the Guttiferae. (As far as I am aware, no counts have been made for species of the Bonnetioideae.) It was concluded that the basic numbers in *Hypericum* form a descending series from 12 to 7, with a possible extension to 6 if the count of 2n = 24 for *H. gentianoides* proved to indicate tetraploidy. No count based on n = 11 had then been made. Tetraploidy had been recorded on the base numbers n = 8, 9 and 10, but not on n = 7 or definitely on n = 12; and higher degrees of polyploidy appeared to be confined in nature to sect. 9. *Hypericum* and were associated with the largely apomictic *H. perforatum* (2n = 32, 48) and its hybrid with the tetraploid subspecies of *H. maculatum* (*H.* x *desetangsii* Lamotte nm. *desetangsii*) (2n = 32, 40, 48).

Counts published subsequently, along with some hitherto unpublished ones made by Dr Mary Gibby, are incorporated in Table 7, which thus includes all the chromosome numbers of *Hypericum* that are known to me at present. Where the correct name is known, it appears in the second column, asterisked if the identification is doubtful. The third column includes names cited in the original publication where they differ from the accepted ones, due to synonymy or misidentification. In the next two columns, asterisked numbers are regarded as wrong or requiring verification. Details in the remaining columns are given only for the counts not cited in Robson & Adams (1968).

When the haploid numbers (n) have been inserted in the evolutionary diagram (Fig. 54), it is clear that the additional records all support the general conclusions in our earlier paper (Robson & Adams, 1968) that: (i) the basic numbers form a descending series from 12 to 7; (ii) polyploids occur on all these basic numbers except 7; (iii) the level of polyploidy is not higher than 4x, except in sects 3. *Ascyreia* and 9. *Hypericum*, in both of which it reaches 6x. The doubt about the ploidy of *H. gentianoides* (n = 12) was due to its advanced morphology; but similar counts for related species make it very likely that 12 is 2x, not 4x. The number n = 6 has, however, recently been recorded in sect. 30. *Spachium* (see p. 166).

The new counts also indicate the rarity of the base number n = 11, which so far has been found only in sect. 3. *Ascyreia*. In sects 1. *Campylosporus*, 26. *Humifusoideum* and 30. *Spachium*, however, some species have n = 12 and others n = 10–7; and so the basic number n = 11 may well be present in some or all of them, and possibly in sect. 29. *Brathys*.

Polyploidy seems to be frequent in sect. 3. *Ascyreia*, where *H. oblongifolium* has both diploid (n = 12) and tetraploid (n = 24, 22) forms; and the only count of *H. monogynum* (n = 21), from a cultivated source, suggests crossing between plants with n = 20 and n = 22. The groups of Chinese and Himalayan species related respectively to *H. kouytchense* and *H. patulum* both seem to be basically tetraploid (n = 18); but *H. augustinii*, which belongs to the *H. patulum* group, is approximately hexaploid (2n = 54), the actual counts having varied from 2n = 54–59. Although Dr Gibby's count of 2n = 50 for *H.* x *moseranum* (*H. patulum* (n = 18) x *H. calycinum* (n = 10)) is not clearly interpretable, it makes Sugiura's earlier count

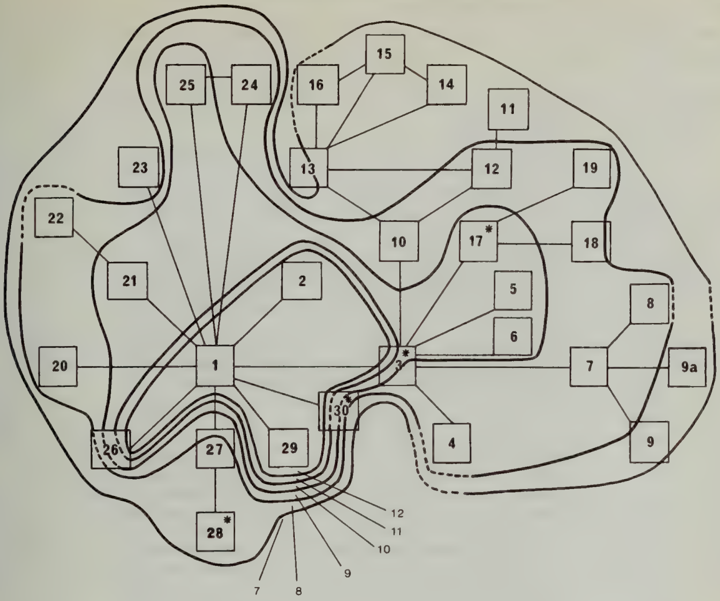

Fig. 54 Distribution of chromosome numbers in *Hypericum*.

NOTE: in sect. 3 there is a secondary basic number (21); in sect. 17, x = 8, 7 may occur, or there may be an ascending series on $x' = 12 \rightarrow 14$; in sect. 28, n = 10 has been recorded. For sections marked*, see text.

of 2n = 36 for this artificial hybrid even more likely to have resulted from misidentification. It is possible that his count for *H. patulum* itself is also based on a misidentification.

Likewise, Dr Gibby's count of 2n = 30 for *H. beanii* 'Gold Cup', which has been grown at Hidcote Manor, Gloucs. under the name *H.* 'Lawrence Johnston', is at variance with Thomas's (1970) count of n = 18 for *H. patulum* 'Gold Cup' (i.e. for the same taxon). The latter count may therefore have been based on a misidentification. This is especially likely as *H. beanii* 'Gold Cup' is the best candidate, on morphological grounds, for the rôle of one parent of *H.* x 'Hidcote', *H. calycinum* being the other (see p. 170). Dr Gibby's count would support this hypothesis, i.e. *H. beanii* 'Gold Cup' (2n = 30) x *H. calycinum* (2n = 20) ⟶ *H.* x 'Hidcote' (2n = 50) (actual counts were c. 48, c. 54).

In sect. 9. *Hypericum* both autopolyploidy (*H. maculatum* subsp. *obtusiusculum*, n = 16) and suspected allopolyploidy (*H. perforatum*, n = 16) are found (Robson, 1958*a*), and a further count of 2n = 32 for *H. undulatum* provides additional evidence that this species does occur in diploid and tetraploid forms. Culwell (1970) observed lagging chromosomes, and consequent variation in haploid number, in *H. punctatum* and *H. pseudomaculatum*, a phenomenon that had already been reported in *H. perforatum* (Nielsen, 1924) and would explain Bell's (1965) record of n = 7 for *H. punctatum*.

The counts of species in sect. 17. *Hirtella* recently made by Reynaud (1973, 1975, 1980) have revealed what appears to be an ascending series of diploid numbers from 2n = 20 (*H.*

Table 7 Chromosome numbers in *Hypericum*

Section	Taxon	Original determination	n
1. Campylosporus	*H. revolutum* Vahl subsp. *keniense* (Schweinf.) N. Robson	*H. keniense*	
	H. revolutum Vahl subsp. *revolutum*		
2. Psorophytum	*H. balearicum* L.		
3. Ascyreia	*H. oblongifolium* Choisy	*H. cernuum*	
	H. oblongifolium Choisy	*H. cernuum*	24
	H. oblongifolium Choisy	*H. cernuum*	22
	H. monogynum L.	*H. chinense*	21
	H. calycinum L.		10
	H. dyeri Rehder	*H. lysimachioides*	10
	H. uralum Buch. -Ham. ex D. Don	*H. patulum*	10
	H. uralum Buch. -Ham. ex D. Don	*H. patulum*	10
	H. x 'Rowallane' (*H. hookeranum* x *leschenaultii*)		
	H. kouytchense H. Lév.		
	H. kouytchense H. Lév.	*H. patulum* 'Sungold'	18
	H. beanii N. Robson	*H. patulum* var. *henryi*	18
	H. beanii 'Gold Cup'	*H. patulum* 'Gold Cup'	18*
	H. beanii 'Gold Cup'	*H.* 'Lawrence Johnston'	
	H. patulum Thunb. ex Murray		18*
	H. forrestii (Chittenden) N. Robson	*H. patulum* var?	18
	H. forrestii (Chittenden) N. Robson	*H. patulum*	18
	H. forrestii (Chittenden) N. Robson		
	H. x *moseranum* André (*H. patulum* x *calycinum*)		18*
	H. x *moseranum* André		
	H. x 'Hidcote' (parentage unknown)		18
	H. x 'Hidcote'		
	H. augustinii N. Robson		
4. Takasagoya	———		
5. Androsaemum	*H. grandifolium* Choisy		
	H. grandifolium Choisy		
	H. grandifolium Choisy	*H. inodorum*	
	H. hircinum L.		20
	H. hircinum L.		
	H. hircinum L.		
	H. hircinum var. *pumilum* hort.		

2n	Authority	Source	Location of voucher
24	I. & O. Hedberg (1977)	Kenya (Mt. Elgon)	UPS
24	Gibby	Malawi (Mt. Zomba)	BM
24	Nilsson & Lassen (1971)	Mallorca	LD
24	R.(obson)& A.(dams) (1968)		
	Sareen, Kant & Pratap (1974)	India (Chandigarh)	PANJAB
	Mehra & Sareen (1969)	India (Naintal)	PANJAB
	Sareen, Kant & Pratap (1974)	India (Chandigarh)	PANJAB
20	R. & A.		
	Mehra & Sareen (1969)	India (Mussoorie)	PANJAB
	Mehra & Sareen (1969)	India (W. Himalaya)	PANJAB
	Sareen, Kant & Pratap (1974)	India (W. Himalaya)	PANJAB
20	Gibby	Chelsea Physic Garden	BM
c.36	Gibby	Chelsea Physic Garden	BM
	Thomas (1970)	Univ. of Alabama Arboretum	
	Thomas (1970)	Arnold Arboretum	
	Thomas (1970)	Univ. of Alabama Arboretum	
30	Gibby	Hidcote Manor (Gloucestershire)	BM
36*	R. & A.		
	Thomas (1970)	Arnold Arboretum	A
	Thomas (1970)	Arnold Arboretum	A
38	Gibby	Chelsea Physic Garden	BM
	R. & A.		
50	Gibby	Chelsea Physic Garden	BM
	Thomas (1970)	Arnold Arboretum	
c.48,c.54,55	Gibby	Chelsea Physic Garden	BM
c.54	Gibby	Chelsea Physic Garden	BM
40	R. & A.		
40	Borgen (1969)	ex Canary Is. (Tenerife)	O
40	van Loon (1974)	Canary Is. (Tenerife)	U
	R. & A.		
40	Reynaud (1975)	Lebanon (Massif du Bedar)	MARS
40	van Loon & de Jong (1978)	Corsica (Ghisoni)	U
40	R. & A.		

Table 7 (contd.)

Section	Taxon	Original determination	n
5. Androsaemum (contd.)	*H.* x *inodorum* Miller	*H. elatum*	20
	H. androsaemum L.		20
	H. androsaemum L.		
	H. androsaemum L.		
6. Inodora	*H. xylosteifolium* (Spach) N. Robson	*H. inodorum*	20
7. Roscyna	*H. ascyron* L.		9
8. Bupleuroides	———		
9. Hypericum	*H. nagasawai* Hayata		18*
	H. kamtschaticum Ledeb. var. *senanense* (Maxim.) Y. Kimura		
	H. erectum Thunb. ex Murray		
	H. graveolens Buckley		16*
	H. graveolens Buckley		8
	H. pseudomaculatum Bush		8
	H. pseudomaculatum Bush		
	H. mitchellianum Rydberg		8(ring)
	H. mitchellianum Rydberg		
	H. punctatum Lam.		8(ring),7
	H. oaxacanum R. Keller* (nomen)	*H. formosum*	8
	H. scouleri Hooker	*H. formosum* var. *scouleri*	8
	H. maculatum Crantz		
	subsp. *maculatum*		8
	subsp. *maculatum*	*H. quadrangulum*	8
	subsp. *maculatum*	*H. fallax*	
	subsp. *maculatum*		8
	subsp. *maculatum*		
	H. maculatum subsp. *obtusiusculum* (Tourlet) Hayek		
	subsp. *obtusiusculum*	*H. erosum*	
	H. x *desetangsii* Lamotte (*H. maculatum* x *perforatum*)		
	nm. *desetangsii*		
	nm. *desetangsii*	*H. desetangsii*	
	H. perforatum L.		16,17,18
	H. perforatum L.		

2n	Authority	Source	Location of voucher
40	R. & A.		
40	R. & A.		
40	van Loon & de Jong (1978)	Ireland (Roscommon)	U
40	Lessani & Chariat-Panahi(1979)	Iran (Mazanderan)	VIL
	R. & A.		
	R. & A.		
	Hsu (1968)		
16	R. & A.		
16	R. & A.		
	R. & A.		
16	Culwell (1970)	U.S.A. (N. Carolina)	NCU
	R. & A.		
16	Culwell (1970)	U.S.A. (Missouri)	NCU
	R. & A.		
16	Culwell (1970)	U.S.A. (N. Carolina)	NCU
	R. & A.		
	R. & A.		
	Kyhos (1967)	U.S.A. (California)	DS
16	R. & A.		
16	Noack (1939)		
16	Schwarz (1965)		JE
	Laane (1969)	Norway (Vestfold)	BG
16	Reynaud (1975)	France (Pyr. Or.)	MARS
32	R. & A.		
16*	Schwarz (1965)		JE
32,40,48	R. & A.		
16*	Schwarz (1965)		JE
32,48	R. & A.		
32	Schwarz (1965)		JE

Table 7 (contd.)

Section	Taxon	Original determination	n
9. Hypericum (contd.)	*H. perforatum* L.		
	H. perforatum L.		
	H. perforatum L.		
	H. perforatum L.		
	H. perforatum L.		
	H. perforatum L.		
	H. perforatum L.		
	H. perforatum L.		
	H. perforatum var. *microphyllum* DC.	*H. veronense*	
	H. perforatum var. *angustifolium* DC.*		12
	H. undulatum Schousb. ex Willd.		8
	H. undulatum Schousb. ex Willd.*		16
	H. undulatum Schousb. ex Willd.*		
	H. undulatum Schousb. ex Willd.	*H. boeticum*	
	H. tetrapterum Fries		8
	H. tetrapterum Fries	*H. acutum*	8
	H. tetrapterum Fries	*H. acutum*	8
	H. tetrapterum Fries		
	H. tetrapterum Fries		
	H. tetrapterum Fries	*H. quadrangulum*	
	H. triquetrifolium Turra		
	H. triquetrifolium Turra		
	H. elegans Stephan ex Willd.		16
9a. Concinna	*H. concinnum* Bentham		16
10. Olympia	*H. olympicum* L.		9
	H. olympicum L.		
	H. olympicum L.		
	H. olympicum L.	*H. polyphyllum*	9
	H. polyphyllum Boiss. & Bal. subsp. *polyphyllum*		
	subsp. *polyphyllum*	*H. olympicum* subsp. *auriculatum* Robson & Hub.-Mor.	
11. Campylopus	*H. cerastoides* (Spach) N. Robson		

2n	Authority	Source	Location of voucher
32	Gadella & Kliphuis (1966)	Netherlands (Utrecht)	U
32	Gadella & Kliphuis (1970)	Italy (Aosta)	U
32	Nilsson & Lassen (1971)	Mallorca	LD
32	Holub, Mesícek & Javurková (1972)	Czechoslovakia (Prague)	PR
32	Reynaud (1973)	Turkey (Izmir)	MARS
32	Löve & Kjellqvist (1974)	Spain (Jaén)	LIVU, LD
32	van Loon & de Jong (1978)	Yugoslavia (Zadar-Rijeka)	U
32	van Loon & Snelders (1979)	Greece (Athos Peninsula)	U
16*	Schwarz (1965)	Austria (Graz)?	JE
	R. & A.		
16	R. & A.		
	R. & A.		
16,32	Sugiura (1940)		
32	Löve & Kjellqvist (1974)	Spain	
16	R. & A.		
	Stenar (1938)	Berlin Bot. Garden	
16	Noack (1939)		
16	Pólya (1950)		
16	Gadella & Kliphuis (1966)	Netherlands (Utrecht)	U
16	Zhukova (1967)		
16	Reynaud (1973)	Turkey (Side)	MARS
16	Reynaud (1975)	Greece (Lidhorikion)	MARS
	R. & A.		
	R. & A.		
	R. & A.		
18	Contandriopoulos & Lanzalavi (1968)		
18	van Loon & de Jong (1978)	Greece (Kavalla-Thessaloniki)	U
	R. & A.		
18	Reynaud (1973)	Turkey (Antalya)	
18	Reynaud (1973)	Turkey (Antalya)	
16	Krusheva (1975)	Bulgaria (Mt. Pirin)	SOA

Table 7 (contd.)

Section	Taxon	Original determination	n
12. Origanifolia	*H. origanifolium* Willd.		9
	H. origanifolium Willd.		
	H. aviculariifolium Jaub. & Spach subsp. *aviculariifolium*		
	H. aviculariifolium subsp. *depilatum* (Freyn & Bornm.) N. Robson		
13. Drosocarpium	*H. vesiculosum* Griseb.		
	H. barbatum Jacq.	*H. barbatum* var. *typicum*	
	H. barbatum var. *trichanthum* (Boiss. & Sprun.) Boiss.		
	H. barbatum var. *pindicola* Hausskn.		
	H. barbatum var. *epiroticum* Hal.		
	H. aucheri Jaub. & Spach		
	H. rumeliacum Boiss.	*H. apollinis*	
	H. rumeliacum Boiss.		7
	H. rumeliacum Boiss.	*H. apollinis*	
	H. rumeliacum Boiss.	*H. apollinis*	
	H. bithynicum Boiss.		
	H. richeri Vill. subsp. *richeri*		7
	H. richeri Vill. subsp. *richeri*		
	H. perfoliatum L.		
	H. montbretii Spach		
	H. spruneri Boiss.		
14. Oligostema	*H. linarifolium* Vahl		
	H. linarifolium Vahl		
	H. humifusum L.		8
	H. humifusum L.		
15. Thasia	———		
16. Crossophyllum	*H. orientale* L.		8
17. Hirtella	*H. hyssopifolium* Chaix	*H. hyssopifolium* subsp. *hyssopifolium*	
	H. lydium Boiss.		
	H. lydium Boiss.		
	H. scabrum L.		
	H. hirtellum (Spach) Boiss.		14
	H. helianthemoides (Spach) Boiss.		
	H. vermiculare Boiss. & Hausskn.		

2n	Authority	Source	Location of voucher
	R. & A.		
18	Reynaud (1973)	Turkey (Içel, Konya)	MARS
18	Reynaud (1973)	Turkey (Antalya)	MARS
18	Reynaud (1973)	Turkey (Içel, Konya)	MARS
16	Reynaud (1980)	Greece (Mt. Tymphrestos)	MARS
16	Contandriopoulos & Lanzalavi (1968)		
16	Contandriopoulos & Lanzalavi (1968)		
32	Contandriopoulos & Lanzalavi (1968)		
14	Reynaud (1980)	Greece (Col de Peiria)	MARS
16	Reynaud (1973)	Turkey (Kaz Dağ)	MARS
16	Contandriopoulos & Lanzalavi (1968)	Greece (Gamila)	MARS
	R. & A.		
14	Reynaud (1975)	Greece (Mt. Vardoussia)	MARS
14	Reynaud (1980)	Greece (Mt. Parnassus)	MARS
14	Reynaud (1973)	Turkey (Bursa)	MARS
	R. & A.		
14	Reynaud (1975)	France (Hte. Loire, Alpes Mar.)	MARS
14	Reynaud (1975)	France (Ile de Port-Cros)	MARS
14	Reynaud (1973)	Turkey (Içel)	MARS
14	Reynaud (1980)	Greece (Hepatochorion)	MARS
16	R. & A.		
16	van Loon & de Jong (1978)	Portugal (S. da Gardunha)	U
16	R. & A.		
16	van Loon & de Jong (1978)	Portugal (S. da Estrella)	U
	R. & A.		
20	Reynaud (1975)	France (Var, Massif Central)	MARS
24	Reynaud (1975)	Turkey	MARS
24	Reynaud (1980)	Turkey (Amanus Mts)	MARS
24	Reynaud (1973)	Turkey (Içel, Konya)	MARS
28	Reynaud (1980)	Iran (Koram Abad road)	MARS
28	Reynaud (1980)	Iran (Col Singal)	MARS
28	Reynaud (1980)	Iran (Col de Assad Abad)	MARS

Table 7 (contd.)

Section	Taxon	Original determination	n
18. Taeniocarpium	*H. hirsutum* L.		9
	H. hirsutum L.		9
	H. hirsutum L.		
	H. kotschyanum Boiss.		
	H. confertum Choisy subsp. *confertum*		
	H. confertum subsp. *stenobotrys* (Boiss.) Holmboe		
	H. linarioides Bosse		
	H. pulchrum L.		9
	H. pulchrum L.		9
	H. pulchrum forma *procumbens* Rostrup		
	H. nummularium L.		
	H. nummularium L.		
	H. saxifragum Robson & Hub.-Mor.		
19. Coridium	*H. empetrifolium* Willd.		9
	H. amblycalyx Coust. & Gand.		9
	H. coris L.		9
	H. coris L.		
20. Myriandra	*H. kalmianum* L.		9
	H. kalmianum L.		
	H. densiflorum Pursh		9
	H. lobocarpum Gatt.	*H. densiflorum* var. *lobocarpum*	9
	H. prolificum L.		9
	H. frondosum Michaux		9
	H. galioides Lam.		9
	H. lissophloeus P. Adams		9
	H. fasciculatum Lam.		9
	H. brachyphyllum (Spach) Steudel		9
	H. reductum P. Adams		9
	H. exile P. Adams		9
	H. myrtifolium Lam.		9
	H. nudiflorum Michaux		9
	H. cistifolium Lam.		9
	H. dolabriforme Vent.		9

2n	Authority	Source	Location of voucher
18	R. & A.		
18	Noack (1939)		
18(+0–1B)	Feràkovà (1972)		
18	Reynaud (1973)	Turkey (Içel)	MARS
18	Reynaud	Turkey (Bursa)	MARS
18	Reynaud	Turkey (Içel, Konya)	MARS
18	Contandriopoulos & Lanzalavi (1968)		
18	R. & A.		
18	Noack (1939)		
18	R. & A.		
18	Reynaud (1975)	Spain (Pyrenees)	MARS
16	Caraz-Billat (1968)	Spain (Pyrenees)	
18	Reynaud (1973)	Turkey (Antalya)	MARS
18	Contandriopoulos & Lanzalavi (1968)		
18	Contandriopoulos & Lanzalavi (1968)		
	R. & A.		
18	Reynaud (1975)	Italy (Liguria)	MARS
	R. & A.		
18	Pringle (1976)	U.S.A. (Michigan)	HAM
	R. & A.		
	R. & A.		
	R. & A.		
	R. & A.		
	R. & A.		
18	R. & A.		
	R. & A.		
	R. & A.		
	R. & A.		
	R. & A.		
	R. & A.		
	R. & A.		
	R. & A.		
	R. & A.		

Table 7 (contd.)

Section	Taxon	Original determination	n
20. Myriandra (contd.)	*H. adpressum* Barton		9
	H. adpressum var. *spongiosum* B.L. Robinson		9
	H. ellipticum Hooker		9
	H. ellipticum Hooker		
	H. microsepalum (Torr. & Gray). A. Gray ex S. Watson.		9
	H. crux-andreae (L.) Crantz	*H. stans*	9
	H. tetrapetalum Lam.		9
	H. hypericoides (L.) Crantz		9
	H. hypericoides subsp. *multicaule* (Michaux ex Willd.) N. Robson	*H. stragulum*	9
	H. suffruticosum Adams & Robson		9
	H. x *arnoldianum* Rehder (*H. lobocarpum* x? *densiflorum*)		9
	H. x *dawsonianum* Rehder (*H. lobocarpum* x *prolificum*)		9
21. Webbia	*H. canariense* L.		
	H. canariense L.		
22. Arthrophyllum	———		
23. Triadenioides	*H. pallens* Banks & Solander		
24. Heterophylla	*H. heterophyllum* Vent.		
25. Adenotrias	*H. aegypticum* L.		10
	H. russeggeri (Fenzl) R. Keller		10
	H. russeggeri (Fenzl) R. Keller		10
26. Humifusoideum	*H. saruwagedicum* Diels	*H. macgregorii*	
	H. peplidifolium A. Rich.		
27. Adenosepalum	*H. glandulosum* Aiton		
	H. reflexum L.f.		

2n	Authority	Source	Location of voucher
	R. & A.		
	R. & A.		
	R. & A.		
c.18	Gillett (1975)	Canada (Quebec)	CAN
18	R. & A.		
	R. & A.		
	R. & A.		
	R. & A.		
	R. & A.		
	R. & A.		
	R. & A.		
	R. & A.		
40	R. & A.		
40	Borgen (1969)	Canary Is. (Tenerife)	O
16	Reynaud (1973)	Turkey (Konya)	MARS
18	Reynaud (1973)	Turkey (Konya)	MARS
	Ornduff in Robson (1977*a*)	Morocco	UC
	Reynaud (in litt. 1978)	Syria (Herife)	MARS
	Reynaud (1980)	Syria (Slenfé)	MARS
24	R. & A.		
16	I. & O. Hedberg (1977)	Ethiopia (Gulama Mts.)	UPS
18	van Loon & de Jong (1978)	Canary Is. (Tenerife)	U
18	Borgen (1969)	Canary Is. (Tenerife)	O

Table 7 (contd.)

Section	Taxon	Original determination	n
27. Adenosepalum (contd.)	*H. reflexum* var. *lanuginosum* Pitard		
	H. coadunatum Chr. Sm.		
	H. coadunatum Chr. Sm.		
	H. pubescens Boiss.		
	H. tomentosum L.		8
	H. delphicum Boiss. & Heldr.		
	H. caprifolium Boiss.		
	H. annulatum Moris		
	H. montanum L.		8
	H. montanum L.		8
	H. montanum L.		
	H. atomarium Boiss.		
	H. lanuginosum Lam. var. *lanuginosum*		
	var. *lanuginosum*		
	H. lanuginosum var. *scabrellum* (Boiss.) N. Robson		
	H. huber-morathii N. Robson		
	H. elodeoides Choisy		8
28. Elodes	*H. elodes* L.		16
	H. elodes L.		10
	H. elodes L.		
29. Brathys	*H. stenopetalum* Turcz.	*H. irazuense*	12
30. Spachium	*H. campestre* Cham. & Schlecht.?	*H.* sp. aff. *paniculatum*	12
	H. drummondii (Grev. & Hook.) Torr. & Gray		12
	H. gentianoides (L.) Britt., Sterns & Poggenb.		12
	H. gentianoides (L.) Britt., Sterns & Poggenb.		12
	H. denticulatum Walter		12
	H. denticulatum Walter var. *denticulatum*		12
	H. denticulatum Walter var. *acutifolium* (Ell.) Blake		12
	H. harperi R. Keller		12
	H. setosum L.		6
	H. cumulicola (Small) P. Adams		6
	H. anagalloides Cham. & Schlecht.		
	H. majus (A. Gray) Britton		8
	H. majus (A. Gray) Britton		8
	H. canadense L.		8
	H. canadense L.		8
	H. canadense L.		
	H. gymnanthum Engelm. & Gray		8

2n	Authority	Source	Location of voucher
18	van Loon & de Jong (1978)	Canary Is. (Tenerife)	U
18	R. & A.		
18	Ortega & Navarro (1978)	Canary Is. (Gran Canaria)	
18	K. Jones (pers. comm.) 1980	R.B.G., Kew	K
	R. & A.		
16	Reynaud (1980)	Greece (Mt. Dirphys)	MARS
16	Löve & Kjellqvist (1974)	Spain (Jaen)	LIVU, LD
16	Reynaud (1980)	Greece (Col de Peiria)	MARS
16	R. & A.		
16	Noack (1939)		
16	Reynaud (1975)	France (Hte Loire)	MARS
16	Reynaud (1973)	Turkey (Izmir)	MARS
16	Reynaud (1973)	Turkey (Antalya)	MARS
32	Reynaud (1980)	Syria (Slenfé)	MARS
16	Reynaud (1973)	Turkey (Antalya)	MARS
16	Reynaud (1980)	Turkey (Korkuteli to Emali)	MARS
	R. & A.		
	R. & A.		
	Dehay (1972)	France (Brenne)	
20	Gibby	Chelsea Physic Garden	BM
	R. & A.		
	Huyhn (1965)	Peru (Cord. de Vilcabamba)	NEU
	Webb (1980)	U.S.A. (Alabama, Mississippi, Tennessee)	TENN
	R. & A.		
	Webb	U.S.A. (Alabama, N. Carolina)	TENN
24†	R. & A.		
	Webb (1980)	U.S.A. (New Jersey, N. Carolina Tennessee)	TENN
	Webb (1980)	U.S.A. (Alabama, N. Carolina, Tennessee)	TENN
	Webb (1980)	U.S.A. (Florida, Georgia)	TENN
	Webb (1980)	U.S.A. (N. Carolina, S. Carolina)	TENN
	Webb (1980)	U.S.A. (Florida)	TENN
16	Gillett (ined.)	Canada (Vancouver I.)	DAO
	R. & A.		
	Webb (1980)	U.S.A.(Vermont), Canada(Quebec)	TENN
	R. & A.		
	Webb (1980)	U.S.A. (New Hampshire, Maine)	TENN
16	Moore (1973)	Eire (Co. Mayo)	
	Webb (1980)	U.S.A. (Alabama, Mississippi, N. Carolina)	TENN

Table 7 (contd.)

Section	Taxon	Original determination	n
	H. mutilum L.		8
	H. mutilum L.		8
	H. boreale (Britton) Bickn.		8
	H. boreale (Britton) Bickn.		8
	H. boreale (Britton) Bickn.		
	H. japonicum Thunb. ex Murray		8
	H. scioanum Chiov.		
	H. gramineum G. Forster		8
	H. gramineum G. Forster	*H.* sp.	

*Identification or count doubtful.
R. & A. Robson & Adams (1968).
†$2n = 24$ in R. & A. was an error for $n = 24$.

hyssopifolium), through $2n = 24$ (*H. lydium*, *H. scabrum*) to $2n = 28$ (*H. helianthemoides*, *H. vermiculare*, *H. hirtellum*). To read the series as a descending one would be inconsistent with morphological and distributional evidence, and it seems unlikely that 24 is a triploid based on 8 and 28 a tetraploid based on 7. Perhaps the occurrence of irregular pollen grains in this section (Fig. 29, p. 119; see also p. 117 and Clarke, 1975) is an indication of abnormalities in the breeding system in sect. *Hirtella*. If it is so, then we may have an explanation of some of the taxonomic difficulties in this section.

The only other count that does not appear to fit into the general evolutionary hypothesis is that of $n = 10$ for *H. elodes* by Dehay (1972); but Dr Gibby has confirmed the occurrence of this number by a mitotic count. My own record ($n = 16$) agrees better with the interpretation (based on morphology and distribution) of *H. elodes* as a derivative of sect. 27. *Adenosepalum* ($n = 9, 8$); but an increase in basic number from 9 to 10 would not seem to be impossible. Only further counts in sects 27 and 28 will solve this problem.

Webb (1980) has recently counted $n = 6$ for two highly evolved species in sect. 30. *Spachium*, *H. setosum* and *H. cumulicola*. Although the numbers $n = 12$ and $n = 8$ have each been recorded several times in this section, no intermediate ones have yet been found ($2n = 18$ for *H. boreale* (Kapoor, 1972), if correct, is likely to be a variant of $n = 8$, not a true intermediate.) The species with $n = 6$ are not related to those with $n = 8$, however, but to *H. denticulatum* ($n = 12, 24$), of which they appear to be derivatives. Apart from the presence of hairs in *H. setosum*, the variation in the line *H. denticulatum*→*H. setosum*→*H. cumulicola* is almost continuous, so that there is little 'room' for extinct forms with intermediate numbers. On the contrary, the change from 12 to 6 appears to have been sudden. How this change occurred remains to be discovered; possibly some form of Robertsonian (centric) fusion is involved.

(*b*) *Chromosome morphology*

Chromosomes of *Hypericum* are small (0·5–2·2 µm long, cf. Robson & Adams (1968), Reynaud (1973, 1975)) and are often difficult to count satisfactorily. For these reasons no studies of chromosome morphology in the genus have been published. Variations in size within a complement do occur, however (cf. Robson & Adams, 1968), and acrocentric chromosomes with satellites have been depicted in *H. kamtschaticum* var. *senanense* (Matsuura & Sûto, 1935). Therefore, although meta- and submetacentric centromeres seem to predominate in the genus, detailed comparative cytological studies might well yield information of evolutionary significance.

2n	Authority	Source	Location of voucher
	R. & A.		
	Webb (1980)	U.S.A. (Alabama, New York, Pennsylvania, S. Carolina)	TENN
	R. & A.		
	Webb (1980)	U.S.A. (New York)	TENN
18*	Kapoor (1972)	Canada (Nova Scotia)	SMUH
	R. & A.		
16	I. & O. Hedberg (1977)	Kenya (Mt. Elgon)	UPS
	R. & A.		
14	R. & A.		

(*c*) *Chromosome irregularities*

In the North American *Hypericum punctatum* (sect. 9. *Hypericum*), Hoar (1931) discovered structural hybridity (a ring of 16 chromosomes at meiosis); and Adams (1962*a*; Robson & Adams, 1968) recorded the same phenomenon in the closely related *H. mitchellianum*. This taxon is morphologically intermediate between *H. graveolens* and the form of *H. punctatum* that grows in the same area, and it hybridises with *H. graveolens* in nature (Culwell, 1970). It may therefore have the parentage *H. graveolens* x *punctatum*. Culwell, however, came to the conclusion that it was a good species. Adams (in Robson & Adams, 1968) counted n = 16 doubtfully for *H. graveolens* but, according to Culwell (1970), now agrees that this count was an error for n = 8; whilst Bell (1965) counted n = 7 for *H. punctatum* without mentioning any ring-formation. The relationships among these three taxa thus appear rather complex and would repay further investigation (see below, p. 168).

Hybridisation in *Hypericum*

(*a*) *Natural hybrids*

Hypericum is not rich in natural hybrids; at least, not many are known. Where intergradation occurs, as it frequently does, it seems from morphological and distributional evidence to be most often due to incomplete speciation. Only two taxa have been shown experimentally to be natural hybrids, but circumstantial evidence for the hybrid origin of some others is strong.

In sect. 9. *Hypericum*, *H. perforatum* is tetraploid (n = 16) and shows signs of a hybrid origin. Thus the pollen is sometimes highly sterile (Noack, 1939) with lagging chromosomes at meiosis (Nielsen, 1924), and the embryo sacs are largely (92%) pseudogamous.* They develop either parthenogenetically (2n = 4x = 32) or rarely after fertilisation (2n = 6x = 48, as the pollen always undergoes normal meiosis, n = 16). Crosses between these forms result in pentaploid plants (2n = 40). This cytological variability is associated with considerable polymorphism throughout the wide distributional range of *H. perforatum*, but the two types of variation have not yet been completely associated. Thus there is an apparent complete range of morphological variation from the typical broad-leaved, large-flowered form to the narrow-leaved, smaller-flowered var. *angustifolium* DC., in which the chromosomes are constantly reported as 2n = 32 (except for the aberrant n = 12 reported by Gagnieu & Wilhelm, 1965). The hexaploids are rare and do not seem to be morphologically distinct. On

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*Myers (1963) found a smaller proportion of pseudogamous embryo sacs in some American populations of *H. perforatum*.

the other hand, the count of 2n = 16 for var. *microphyllum* DC. (= *H. veronense*) suggests that, as Schwarz (1965) concluded, this taxon may not belong to *H. perforatum* after all.

From the above date it seems that *H. perforatum* may have resulted from an ancient hybridisation between two diploids with subsequent chromosome doubling. If this is indeed its origin, then one parent is almost certainly *H. maculatum* subsp. *maculatum* (n = 8), which is distributed from central Siberia to the Pyrenees. On morphological and geographical grounds the other parent could well be *H. attenuatum* Choisy. Although its chromosome number has not yet been counted, this species has the characters of *H. perforatum* that are absent from *H. maculatum*, and its distribution (in north-east Asia) overlaps that of the latter.

Owing to its pseudogamously produced ovules (n = 4x) and normally reduced pollen (n = 2x), the tetraploid *H. perforatum* produces triploid hybrids with diploids (*H. maculatum* subsp. *maculatum*, *H. tetrapterum*) as ovule parent and pentaploids when they are the pollen parent (Noack, 1939, 1941). With the autotetraploid *H. maculatum* subsp. *obtusiusculum* (cf. Robson 1957, 1958*a*, 1972*b*), it usually produces tetraploid hybrids, which back-cross easily to either parent; but, on the rare occasions when an aposporous embryo sac of *H. perforatum* is fertilised, a hexaploid hybrid can occur (Fig. 55). The tetraploid F_1 hybrids (*H.* x *desetangsii* Lamotte nm. *desetangsii*) are intermediate between the parents; but back-crossing results in a continuous morphological series between them. On the other hand, whereas the triploid form of *H. maculatum* subsp. *maculatum* x *perforatum* (*H.* x *desetangsii* nm. *carianthiacum* (Fröhl.) N. Robson) is recognisably intermediate (Fröhlich, 1960), the pentaploid form (H. x *desetangsii* nm. *perforatiforme* (Fröhl.) N. Robson*) is almost indistinguishable from *H. perforatum*.

As has already been mentioned (p. 167), sect. *Hypericum* also contains two structural hybrids, the N. American *H. punctatum* and *H. mitchellianum*. The latter hybridises in

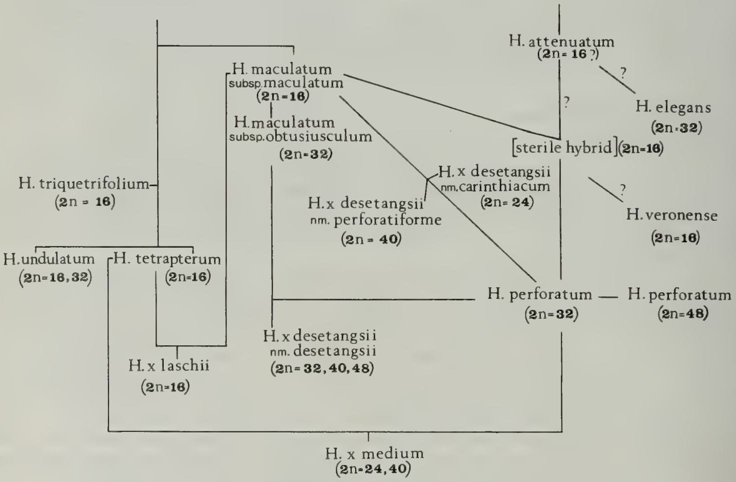
H. attenuatum
(2n = 16 ?)
?
?
H. elegans
(2n = 32)
H. maculatum
subsp. maculatum
(2n = 16)
H. maculatum
subsp. obtusiusculum
(2n = 32)
[sterile hybrid] (2n = 16)
H. x desetangsii
nm. carinthiacum
(2n = 24)
?
H. veronense
(2n = 16)
H. triquetrifolium
(2n = 16)
H. x desetangsii
nm. perforatiforme
(2n = 40)
H. undulatum
(2n = 16, 32)
H. tetrapterum
(2n = 16)
H. perforatum
(2n = 32)
H. perforatum
(2n = 48)
H. x desetangsii
nm. desetangsii
(2n = 32, 40, 48)
H. x laschii
(2n = 16)
H. x medium
(2n = 24, 40)

Fig. 55 Suggested relationships in the *Hypericum perforatum* group.

***H.** x **desetangsii** Lamotte nm. **perforatiforme** (Fröhl.) N. Robson, **comb. et stat. nov.**, Basionym: *H.* x *carinthiacum* *α perforatiforme* Fröhl. in *Mitt. Nat. Ver. Steiermark* **51** : 229 (1915).

nature with *H. graveolens* (Culwell, 1970) and is morphologically intermediate between *H. punctatum* and *H. graveolens*. Culwell crossed these species, but did not continue observing the resultant (healthy) seedlings until they reached maturity.

In sect. 5. *Androsaemum*, the hybrid *H.* x *inodorum* Miller (*H. hircinum* x *androsaemum*) occurs in France and Spain, where the distributions of its parents overlap. It is intermediate in form between them. In gardens, where it appears to have arisen independently more than once in the 18th century (and later ?), it is much more variable, because the smaller forms of *H. hircinum* from various parts of the Mediterranean region (especially from the Balearic Islands) have crossed with different forms of the variable *H. androsaemum*. There is no apparent cytological barrier; both species have $2n = 4x = 40$ and there is no evidence of reduced fertility in the hybrids (cf. Robson, 1975).

In sect. 14. *Oligostema*, *H. humifusum*, *H. linarifolium* and *H. australe* form a 'superspecies' in which intermediates occur where the component species overlap in distribution. Although it is not yet clear whether the intermediates are due to hybridisation or incomplete separation, Druce gave intermediates between *H. humifusum* and *H. linarifolium* from the Channel Islands the name *H.* x *caesariense* without validating it (cf. Robson, 1975). There appears to be a series of forms linking these species, both of which are diploids with $2n = 16$ chromosomes. On the other hand, the record from Germany of the intersectional hybrid *H. humifusum* x *perforatum* (*H.* x *assurgens* Peterm., nomen) (Kuntze, 1880) is based on a misidentification. The specimen appears to be a depauperate example of *H. perforatum*. Such a 'wide' cross would be unlikely to survive in a natural habitat.

In sect. 20. *Myriandra*, where the known chromosome numbers are all $n = 9$, Rehder (1910) reported three alleged hybrids growing spontaneously in the Arnold Arboretum, Mass., U.S.A., which he named respectively *H.* x *arnoldianum* (*H. lobocarpum* x *galioides*), *H.* x *dawsonianum* (*H. lobocarpum* x *prolificum*) and *H.* x *nothum* (*H. kalmianum* x *densiflorum*). After studying Rehder's specimens, however, Adams (1972) concluded that only *H.* x *dawsonianum* had been assigned to the correct parentage. The plants of the latter and of *H.* x *arnoldianum* were fertile and showed no cytological irregularity or pollen sterility (Hoar & Haertl, 1932). On the bases of their intermediate morphology, Adams agreed that the parentage of *H.* x *dawsonianum* appeared to be *H. lobocarpum* x *prolificum*, but thought that that of *H.* x *arnoldianum* was *H. densiflorum* x *lobocarpum*, not the more distantly related *H. galioides* x *lobocarpum*. Adams decided that Rehder's specimens of *H.* x *nothum* were assignable to *H. densiflorum* itself, not to *H. densiflorum* x *kalmianum*. Likewise, he concluded that *H.* x *vanfleetii*, a name which Rehder (1940) applied to a horticultural form intermediate between *H. prolificum* and *H. frondosum*, was not based on hybrid material but on an extreme form of *H. prolificum*. It is quite likely, however, that these last-named species, as well as other members of sect. 20. *Myriandra* not discussed above, can and do hybridise in cultivation; but, according to Adams, there appears to be very little interspecific hybridisation in nature among the woody members of this section.

Finally, in sect. 30. *Spachium* natural hybridisation has been reported among some of the herbaceous species. The evidence is circumstantial; but it seems likely on morphological and distributional grounds that (i) *H.* x *dissimulatum* Bickn. (from Massachusetts, U.S.A.) is the result of crosses between *H. canadense* and *H. mutilum* or *H. boreale* (cf. Fernald, 1947 : 87; Webb, 1980*) and (ii) that *H. gramineum* and *H. japonicum* hybridise where their areas of distribution overlap in Bhutan (cf. Robson, 1973*a*).

(*b*) *Artificial hybrids*

These have been confined mainly to two sections: 3. *Ascyreia*, where they have been produced for horticultural purposes, and 9. *Hypericum*, where their genetics, breeding systems and morphology have been studied. In both sections, hybrids that are the result of wide crosses are likely to lack chlorophyll to some extent, at least in the seedling stage.

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*Webb (1980), on the bases of morphological intermediacy and reduced pollen stainability, recorded the following hybrids: *H. boreale* x *canadense*, *H. boreale*? x *majus*, *H. canadense* x *gymnanthum*?, *H. canadense* x *majus*, *H. canadense* x *mutilum*, *H. majus* x *mutilum*. He regards *H.* x *dissimulatum* as including recurrent hybrids of both *H. canadense* x *mutilum* and *H. boreale* x *canadense*.

(i) Sect. *Ascyreia*.

(α) *H.* x *moseranum* Luquet ex André (1889). This plant was the result of the first recorded hybridisation in sect. *Ascyreia*, made by Moser, a nurseryman at Versailles. He crossed *Hypericum patulum* ♀ (introduced to Europe from Japan by Oldham in 1862) with *H. calycinum* L. ♂. The resultant hybrid was intermediate between the parents and apparently fertile. It has become popular in gardens. Considering the parental chromosome numbers (respectively $2n = 36, 20$), it would be expected to have $2n = 28$; but Sugiura (1944) recorded $n = 18$, whereas Dr Mary Gibby found $2n = c.\ 50$ (see Table 7, p. 152). The former count may have been based on a misidentification, but the latter suggests some cytological instability in the hybrid. Genetical instability no doubt produced the sport with variegated (white- to pink-margined leaves) which Maumené named var. *tricolor* and Rehder reduced to a forma. The correct category, of course, is nothomorph.* The leaves and flowers are smaller and appear less healthy than those of nm. *moseranum*.

(β) *H.* x 'Hidcote'. When this plant was first sent to a Royal Horticultural Society's show, where it was exhibited by Hilling's Nursery, Chobham, Surrey, it was said to have been possibly introduced from Yunnan by Lawrence Johnston, the owner of Hidcote Manor, Gloucestershire (Synge, 1950). Other suggested sources of introduction have been (i) the famous collector of Himalayan plants George Forrest and (ii) an East African garden (cf. Fletcher, 1955). I have, however, seen no specimens from a wild source. An origin by hybridisation at Hidcote seems much more likely (cf. Robson, 1970). This possibility was also mentioned in 1950. The records at Hidcote Manor of the origin of their plants have unfortunately been lost (Head Gardener, Hidcote Manor, 1961, pers. comm.). On the other hand, Stern (1960) stated that his *Hypericum* x 'Hidcote' plants were produced from cuttings received from W. Miller-Christy of Watergate, Chichester, Sussex in the 1920s. At any rate, *H.* x 'Hidcote' behaves like a hybrid. The pollen is mostly sterile (cf. Thomas, 1970; also P. Dummer, pers. comm.), with lagging univalents at meiosis of the pollen-mother-cells, and seed is never set, the whole flower falling after the petals and stamens have been shed. If it is a hybrid, then the relatively densely reticulate leaf-venation, large sepals and long styles, together with its hardiness, suggest that one parent is probably *H. calycinum*. The identity of the other parent, however, is still in doubt.

At first I thought that *H. forrestii* could be the missing parent (Robson, 1970) and encouraged two hybridisers, Mr Donald Walker, North Mymms, Hatfield, Herts. and Mr Peter Dummer of Hilliers' Nurseries, Winchester, Hants, to make the cross *H. forrestii* x *calycinum*. Both hybridisers produced plants that incorporate certain of the characters of *H.* x 'Hidcote', some of which look superficially like it; but neither set of progeny contained an exact match for it. In particular, although its deep orange anthers appeared in some of the seedlings, in none were the stamen filaments as short as they are in *H.* x 'Hidcote'. It would seem, then, that the other parent of the latter is likely to be a short-stamened species.

On a recent visit to Hidcote Manor, I found that the plant known to me as *H. beanii* 'Gold Cup' was being grown there under the name *H.* 'Lawrence Johnston'. The only other members of sect. 3. *Ascyreia* in the garden were *H. calycinum* and *H.* x 'Hidcote'. It then occurred to me that *H. beanii* 'Gold Cup' was morphologically suitable to have been the other parent of *H.* x 'Hidcote'. It has the narrower, more acute leaves and the shorter stamens that that parent must have had, and its other characters are also suitable. From plants of *H.* 'Lawrence Johnston' (obtained through the kindness of Mr P. Nichols, the Head Gardener at Hidcote Manor), Dr Gibby was able to make a chromosome count of $2n = 30$, thus establishing that this taxon is fit cytologically to be a parent of *H.* x 'Hidcote' (see p. 151).

***H.* x moseranum** nm. **tricolor** (Maumené) N. Robson, **stat. nov.**
H. x *moseranum* var. *tricolor* Maumené in *Le Jardin* **8** : 186 (1894).
H. x *moseranum* forma *tricolor* (Maumené) Rehder, *Man. Cult. Trees & Shrubs* : 463 (1949).

From the above considerations, then, it seems very likely that *H.* x 'Hidcote' arose (or was created ?) at Hidcote Manor as a hybrid between *H. calycinum* and *H. beanii* 'Gold Cup'. The true status of the latter taxon remains to be determined.

H. x 'Hidcote', like *H.* x *moseranum*, has given rise to a variegated form. As they age, most plants of this hybrid produce shoots bearing narrow variegated leaves, a phenomenon which has been interpreted by several horticulturalists as indicating genetic deterioration of the clone (cf. Bean, 1973) or a virus attack. Propagation from these shoots results in weakly plants with small flowers comparable with those of *H.* x *moseranum* nm. *tricolor*, but more erect and with no pink tinges in the white areas of the leaf.

(γ) Other hybrids. The only other hybrid in sect. 3. *Ascyreia* that is known to me is *Hypericum kouytchense* x *calycinum*, also made by Mr Donald Walker. He reports that the petals of the hybrid open tardily or even remain imprisoned in the calyx, and the capsules do not turn red like those of *H. kouytchense*. The flowers, however are larger than in that species, and the hybrid set apparently ripe seed.

(ii) Sect. *Androsaemum*. The parentage of *H.* x *indorum* Miller (*H. hircinum* x *androsaemum*) was deduced from circumstantial evidence, viz. intermediate morphology, occurrence in nature within the common distributional area of both parents, and the correspondence of various cultivated forms to variations in the parents (Robson, 1973*b*). Artificial crosses of *H. hircinum* and *H. androsaemum* have, however, also yielded plants indistinguishable from *H.* x *inodorum* (G. Thomas, 1971, pers. comm., D. Walker, 1973, pers. comm.). Mr Walker has been growing seedlings resulting from selfing *H.* x *inodorum* in order to study the segregation, but his results are not yet to hand.

(iii) Sect. *Hypericum* and intersectional hybrids.

(α) Hybrids not involving *H. perforatum*. The discovery of variegation in some experimentally produced *Hypericum* hybrids (Fahrenholtz, 1927) led to extensive hybridisation studies in the genus by Noack (1930–1941) and Herbst (1935). These were concerned mainly with *H. tetrapterum* ('H acutum'), *H. maculatum* subsp. *maculatum* ('H. quadrangulum') and *H . perforatum*, all in sect. 9. *Hypericum*, but also involved wider crosses with *H. calycinum* (sect. 3. *Ascyreia*), *H. olympicum* ('H. polyphyllum') (sect. 10. *Olympia*), *H. rumeliacum* (sect. 13. *Drosocarpium*), *H. pulchrum* and *H. hirsutum* (sect. 18. *Taeniocarpium*) and *H. montanum* (sect. 27. *Adenosepalum*). Excluding those involving *H. perforatum*, which require special consideration, the results of these hybridisations may be summarised as follows (Fig. 56):

(1) Crosses involving different chromosome numbers either set no seed or occasionally resulted in seedlings only.

(2) Crosses involving the same chromosome number sometimes set seed. Intrasectional ones succeeded (sect. 9. *Hypericum*) or not (sect. 18. *Taeniocarpium*); but the only successful 'wide' crosses involved *H. montanum* and *H. tetrapterum*. In all these crosses the fertility was more or less low, and reciprocal ones sometimes behaved differently. This was particularly noticeable with regard to the type, distribution and persistence of variegation in the hybrids, a circumstance which led to controversy (cf. Correns, 1931). Herbst (1935), following his teacher Renner, interpreted the various variegations in terms of the ability of chloroplasts transferred to the ovule parent via the pollen tube to develop chlorophyll in alien cytoplasm. Noack (e.g. 1937*a*, *b*), however, denied that all the variations could be explained thus. The matter seems never to have been resolved satisfactorily.

Variegation is not always a sign of hybridity in *Hypericum*. As Herbst pointed out, it may be due to growth in an unfavourable habitat; and it has also been found in natural conditions which did not appear unfavourable, e.g. in *H. elegans* (sect. 9. *Hypericum*) (Pringsheim & Schwarz, 1933).

(β) *H. perforatum* and its hybrids. Herbst (1935) was cautious in interpreting his hybridisations involving *Hypericum perforatum*, suspecting some irregularity in the breeding system, and Noack (1939, 1941) confirmed his suspicions.

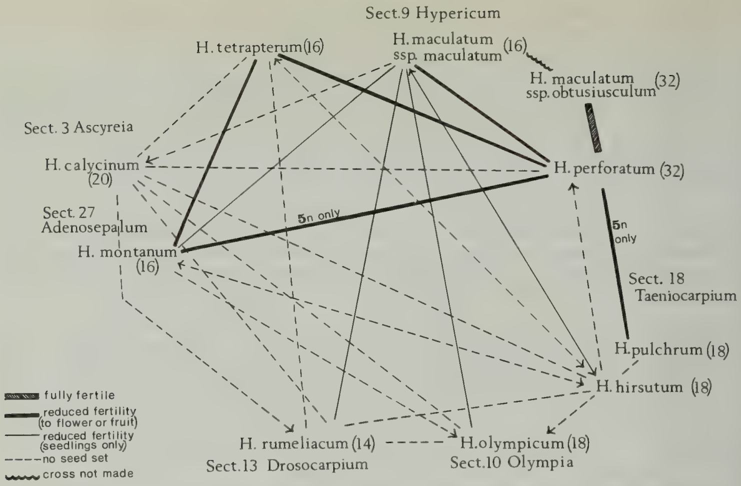
Sect.9 Hypericum
H. tetrapterum (16)
H. maculatum ssp. maculatum (16)
H. maculatum ssp. obtusiusculum (32)
Sect. 3 Ascyreia
H. calycinum (20)
Sect. 27 Adenosepalum
H. montanum (16)
5n only
H. perforatum (32)
5n only
Sect. 18 Taeniocarpium
H. pulchrum (18)
H. hirsutum (18)
H. rumeliacum (14)
Sect.13 Drosocarpium
H. olympicum (18)
Sect.10 Olympia
fully fertile
reduced fertility (to flower or fruit)
reduced fertility (seedlings only)
no seed set
cross not made

Fig. 56 Summary of experimental crosses carried out by Fahrenholtz (1927), Noack (1930–41) and Herbst (1935). The nomenclature used by these authors has been amended.

H. perforatum proved to have a largely apomictic form of reproduction, but to require pollination before seeds would set, i.e. it is pseudogamous. This is due to the almost invariable need to fertilise the endosperm nucleus before the embryo can develop. Both sexual and aposporous embryos have the same chromosome number ($2n = 32$), so that the only means of determining the method of reproduction is by counting the chromosome number of the endosperm nucleus: $16 + 16 + 16 = 48$ in a sexually produced seed, $32 + 32 + 16 = 80$ in an aposporous one.

Since *H. perforatum* is tetraploid, its aposporous embryo sacs are tetraploid and its pollen diploid. Therefore as mentioned above (p. 168), in crosses with diploids with $n = 8$ or 9 the number of the hybrid differs according to whether *H. perforatum* is the pollen parent ($2n = 3x = 16 + 8$ or $9 = 24$ or 25) or the ovule parent ($2n = 5x = 32 + 8$ or $9 = 40$ or 41). Since *H. perforatum* contributes respectively twice and four times as many chromosomes as does the diploid parent, it is not surprising that Noack found the hybrids to be more similar morphologically to *H. perforatum* or, in the case of some of the pentaploids, indistinguishable from it (cf. Fig. 55).

Neither Noack nor Herbst was aware that *H. maculatum* includes plants with two different chromosome numbers ($n = 8, 16$), those with $n = 16$ being autotetraploid (Robson, 1956, 1957). Spontaneous hybrids between the latter (subsp. *obtusiusculum* (Tourlet) Hayek) and *H. perforatum* are common, the progeny being apparently fully fertile (*H.* x *desetangsii* nm. *desetangsii*); and this hybrid has also been produced experimentally (cf. Robson, 1975).

(γ) Other artificial hybrids. Myers (1963) crossed *H. perforatum* and *H. punctatum* (sect. 9. *Hypericum*), *H. frondosum* (diploid and colchicine-induced tetraploid) and *H. prolificum* (sect. 20. *Myriandra*), *H. floribundum* (= *H. canariense*, sect. 21. *Webbia*), and *Triadenum virginicum* in all combinations. He obtained seedlings from the *H. frondosum* x *prolificum* cross (possibly in both directions), but not from the other crosses.

10. Distribution

Introduction

It is a truism to state that meaningful phytogeographic studies can be made only on monophyletic taxa; and it was partly for this reason that *Hypericum* (a clearly monophyletic genus) was chosen for study. It was also for this reason that I have endeavoured to discover the evolutionary trends in the genus as a whole, as well as in each section of it. For, even though recognition of some of the sections (e.g. 22. *Arthrophyllum*, 28. *Elodes*) has resulted in paraphyly, these sections themselves are monophyletic with regard to their immediate ancestors (for the above sections respectively 21. *Webbia* and 27. *Adenosepalum*). The only exception would appear to be sect. 9. *Hypericum*, where it now appears that *H. concinnum* Bentham (endemic to the mountains of central California) is related to a different part of sect. 7. *Roscyna* from that which gave rise to the rest of the section. It is therefore necessary to place this species in a monotypic section.*

It is also true that, whilst merely plotting the distribution of a monophyletic taxon may produce a pattern that is suitable for phytogeographical analysis, the introduction of cladistic considerations (e.g. arrows indicating morphological trends) will make the distribution map more meaningful. Although it may seem self-evident that a geographical replacement series of taxa showing correlated primitive to derived characters gives an indication of the direction of evolutionary development, some authors have taken a contrary view (see Ball, 1976). They argue that the derived forms force the ancestral ones to peripheral areas. Ball (1976 : 420) himself finds it difficult to decide *a priori* between these two possibilities, as indeed it may be in an isolated instance. However, where repeated geographical trends form a logical pattern in a monophyletic taxon, as they do in *Hypericum*, it seems safe to assume that they do indicate evolutionary progressions; and where these patterns are interrupted by wide areas of ocean, they can throw light on aspects of the geological history of the earth. In such cases, Hennig's Phylogenetic Intermediate and Multiple Sister-group Rules and Ashlock's Drift Sequence Rule may be applied (Ashlock, 1974).

There is no essential difference between a geographical trend with gaps in distribution (possibly resulting in speciation) and one in which the changes take place gradually over a continuous area within a single species (although, here, 'continuous' is a relative term). The continuous area must have resulted from gradual colonisation (dispersal) and the gaps from disruptive processes such as extinction, mountain-formation and continental rifting (producing vicariance). If a third process, namely long-distance dispersal, is involved, then a disruption of the logical pattern mentioned above is to be expected. Thus, the (mainly zoological) argument between the proponents of 'vicariance' and 'dispersal' (cf. Croizat, Nelson & Rosen, 1974; Ball, 1976) would appear to be the old one of the role of long-distance dispersal in explaining wide disjunctions in distribution, as the other two 'theories' (dispersal and vicariance) really concern two aspects of the same phenomenon. Since gradual dispersal is the normal means of area extension, then 'Occam's Razor' would preclude the invocation of a hypothesis of long-distance dispersal unless a given distribution is not explicable in terms of normal dispersal. The proponents of the 'vicariance' theory (e.g. Nelson, 1976) are at pains to contrast it with ideas of 'centre of origin', suggesting that apparent centres from which related taxa (e.g. species in a genus) radiate result from vicariance rather than from gradual dispersal. If, however, dispersal and evolutionary diversification from a localised area are followed by isolation of populations, the concept of 'centre of origin' seems to be quite valid. The gradual dissection of a distributional area with time often results in the most primitive taxa in an evolutionary progression having a reduced, relict

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***Hypericum** sect. 9a. **Concinna, sect. nov.** Sectioni 9. *Hypericum* affinis, sed foliis concoloris, saepe conduplicatis vel falcatis, interdum nigropunctatis; sepalis magnis imbricatis inaequalis, interdum nigropunctatis; antheris connectivo succinoglanduloso; differt.
TYPE: *H. concinnum* Bentham.
DISTRIBUTION: California.
1 species.
Basic chromosome number: 8; ploidy 2x.

Table 8 Distribution of the Guttiferae

	North & Central America	South America	Europe, temp. Asia & N. Africa	Trop. & South Africa	Madagascar & Mascarenes	India & Sri Lanka	S.E. Asia & Malaysia	Australia & New Zealand	New Caledonia	Rest of Australasia
Bonnetioideae										
Ploiarium							X			
Bonnetia	X	X								
Marila	X	X								
Other genera (8)		X								
Calophylloideae										
Mesua						X	X			
Calophyllum	X	X		X	X	X	X	X	X	X
Paramammea					X					
*Mammea**	X	X		X	X	X	X		X	X
Endodesmia				X						
Lebrunia				X						
Poeciloneuron						X				
Moronobeoideae										
Pentadesma				X						
Montrouziera									X	
Symphonia	X	X		X	X					
Other genera (4)		X								
Clusioideae										
Decaphalangium		X								
Allanblackia				X						
*Garcinia**	X	X		X	X	X	X	X	X	X
Clusia & 4 other genera	X	X								
Remaining genera (4)		X								
Hypericoideae										
Vismia	X	X		X						
Psorospermum				X	X					
Harungana				X	X					
Eliea					X					
Cratoxylum							X			
Triadenum	X		X			X				
Thornea	X									
Santomasia	X									
Hypericum	X	X	X	X	X	X	X	X	X	X

*Garcinia includes *Rheedia*, *Ochrocarpus* sect. *Paragarcinia*, *Pentaphalangium*, *Tripetalum* and *Septogarcinia*. *Mammea* includes *Ochrocarpus* sect. *Ochrocarpus* (Jones, 1980).

area, those immediately derived having several isolated areas, and the more advanced having larger, more continuous areas (cf. Fig. 7, p. 72; Kubitzki, 1977). These three types of taxa may occupy areas in a linear sequence, in which case the 'centre of origin' is at one end of the sequence; or they may occupy concentric areas, in which case the centre of origin is a true centre. In both cases, dispersal and vicariance are involved.

In *Hypericum* there are many examples of long-distance vicariance, some of which are trans-oceanic; and they cannot all be explained by the same hypothesis, whether it be gradual dispersal and vicariance or long-distance dispersal.

Distribution of the subfamilies of the Guttiferae

(*a*) *Moronobeoideae and Bonnetioideae*

The subfamilies of the Guttiferae show vicariance to varying extents, some of their distributions indicating great age (Table 8). This can be said with confidence in some groups (e.g. the Moronobeoideae—tropical America, tropical Africa and Madagascar, New Caledonia), owing to the size and weight of their fruits; whilst, even where the seeds are small and partially winged, there is no evidence that they are adapted to, or have undergone long-distance dispersal (e.g. the Bonnetioideae—tropical America, Malaysia). Apart from the Hypericoideae, the other subfamilies (Calophylloideae and Clusioideae) are both pantropical and more-or-less heterogeneous and will not be considered further here.

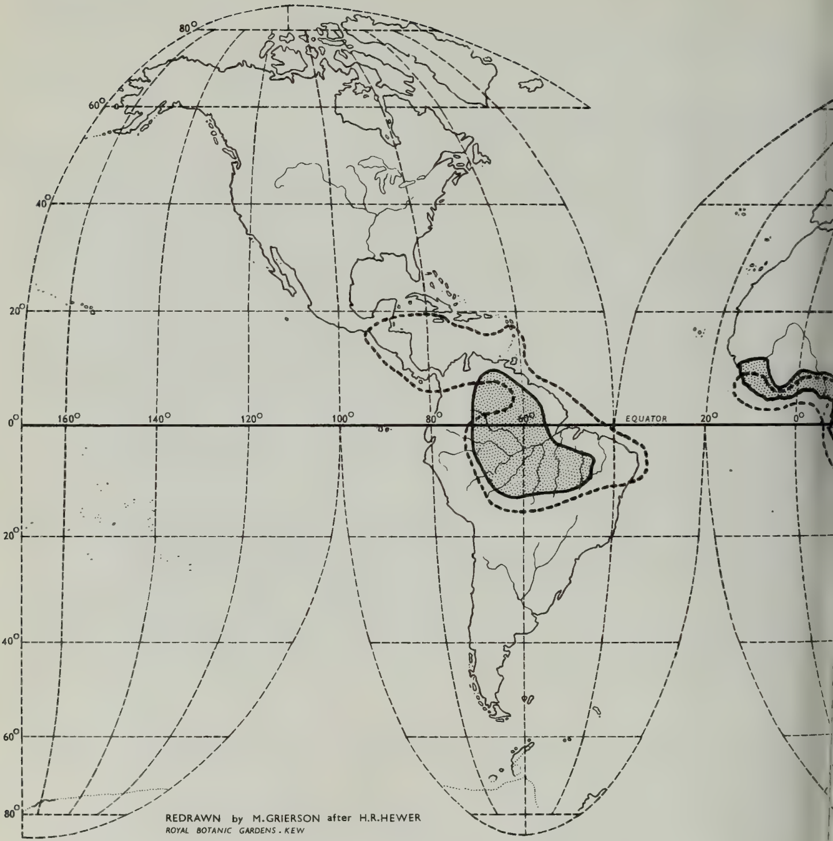
In the Moronobeoideae (Fig. 57) the most primitive genera (*Pentadesma*, *Montrouziera*) are the farthest apart spatially (Africa: Guinea-Congo and New Caledonia, respectively), and one of the most advanced (*Symphonia*) has one species which occurs widely in the tropics of both sides of the Atlantic and several derived species in Madagascar. The intermediate genera are all tropical American. There thus appears to have been an initial east-west divergence that isolated *Pentadesma* and *Montrouziera* from each other and from the rest of the subfamily, followed by evolution to generic level in tropical America (5 genera) with one of these genera (*Symphonia*) spreading back eastwards to Africa and Madagascar. It speciated in Madagascar, but not elsewhere.

In the Bonnetioideae (Fig. 58) the trends are less clear, because all the genera except one are in tropical America. As we have seen, some of these (e.g. *Neblinaria*) are relicts which retain some very primitive characters such as the virtual lack of a leaf midrib. In other respects, however, the most primitive genus is the isolated one, *Ploiarium*, which has one species (*P. alternifolium* Vahl) in southern Thailand, Malaya, northern Sumatra and northern Borneo, and a second (*P. sessilis* Scheffer) in extreme-western New Guinea. It is possible to see these two groups—the American and the Malaysian—as the result of an ancient east-west divergence; but there is not enough evidence to indicate the area from which this divergence occurred.

(*b*) *Hypericoideae*

It was suggested above (p. 64) that the three tribes of the Hypericoideae were respectively related to different parts of the Bonnetioideae, and their distributions and trends bridge the gap in the latter's distribution.

The Vismieae, which are closest to the mainly Amazonian genus *Caraipa*, is itself primitively Amazonian in *Vismia*. Thence this genus extends to nearly all parts of tropical America (except the West Indies north of Tobago) and into tropical Africa, where there occur two groups of species each related to a different American species (Robson, ined.). Each group has given rise to a genus with modified fruit; in one (*Harungana*), each of the five multi-seeded loculi has become a pyrene (i.e. has a hard endocarp), whereas in the other (*Psorospermum*) each loculus has become one-seeded. Both genera occur in Madagascar, and *Harungana* extends into the Mascarenes (Mauritius); but *Harungana* has scarcely speciated (two species), whereas *Psorospermum* has five species on the African mainland (Bamps, 1966) and a considerably larger number in Madagascar, all or mostly epibiotic.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REDRAWN by M.GRIERSON after H.R.HEWER
ROYAL BOTANIC GARDENS - KEW

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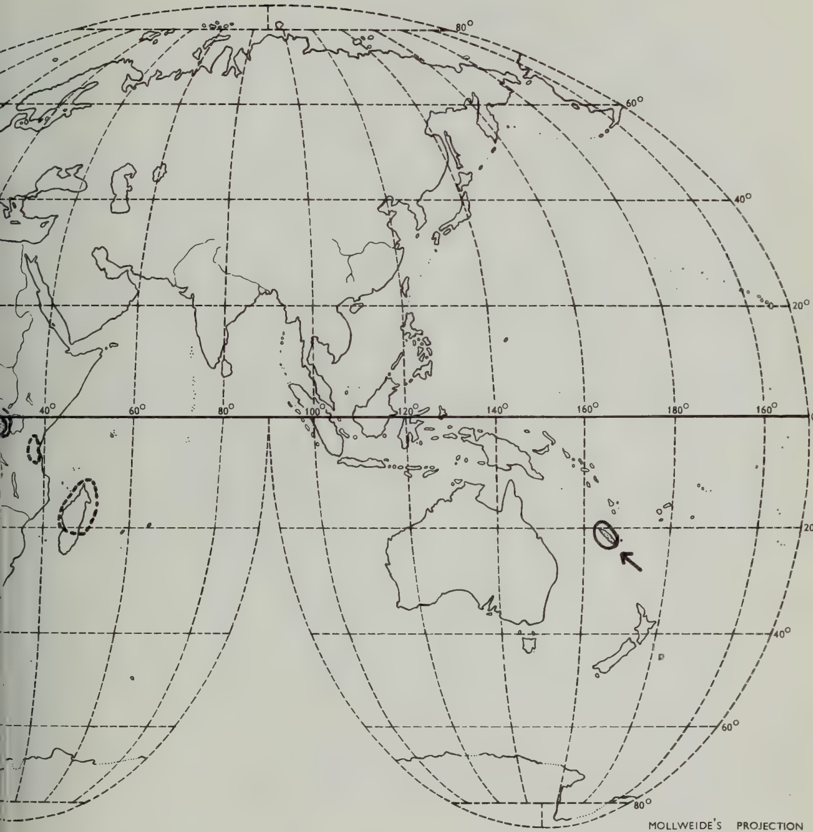
Fig. 57 Distribution of the Moronobeoideae ▬ ▬ *Symphonia,* ▨ other genera.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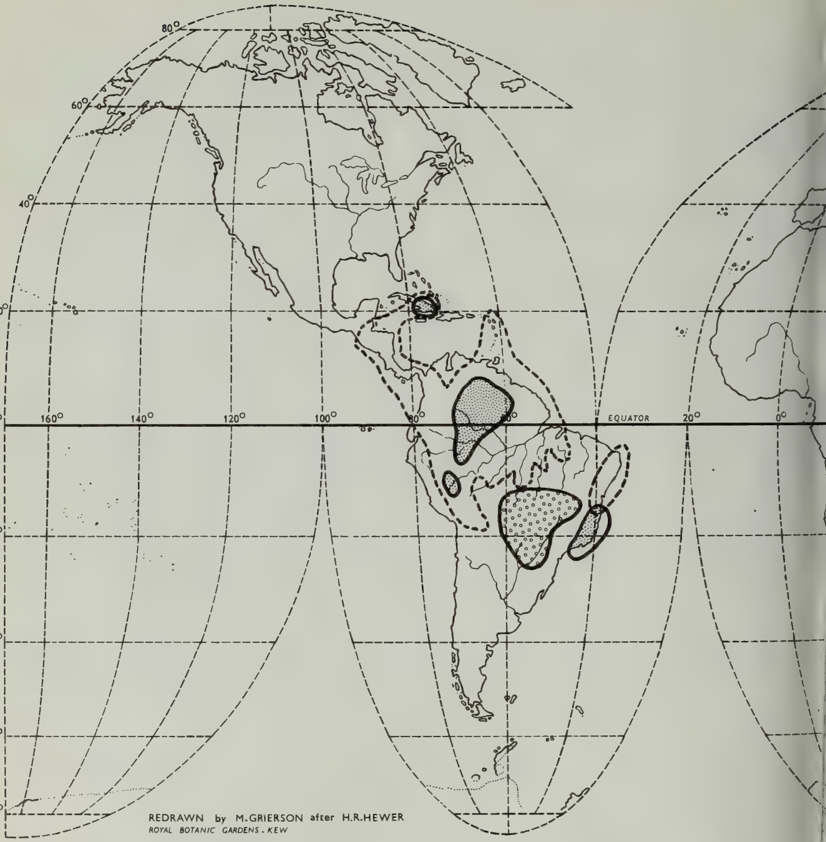
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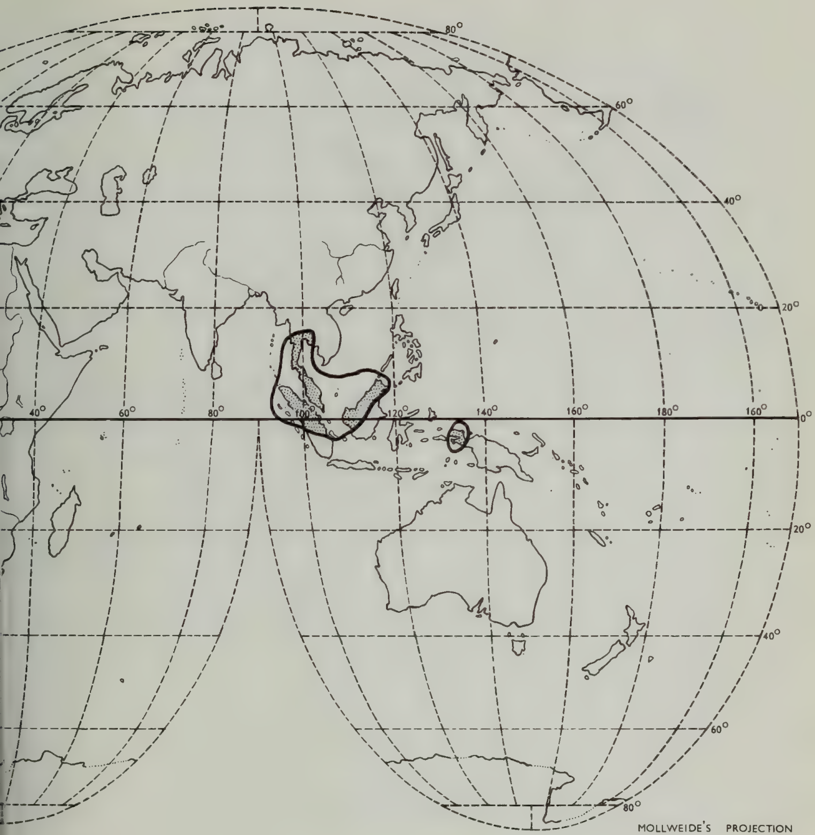
Fig. 58 Distribution of the Bonnetioideae: ⁙⁙⁙ Bonnetioid genera, – – – Caraipoid genera, ⁘⁘⁘ *Kielmeyera*.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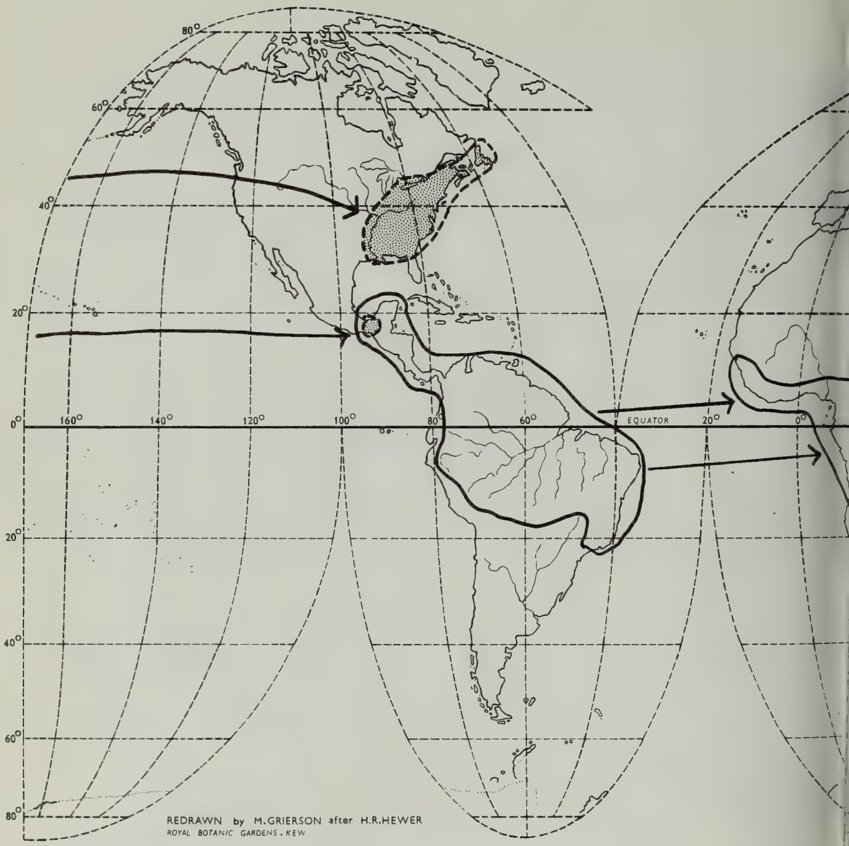
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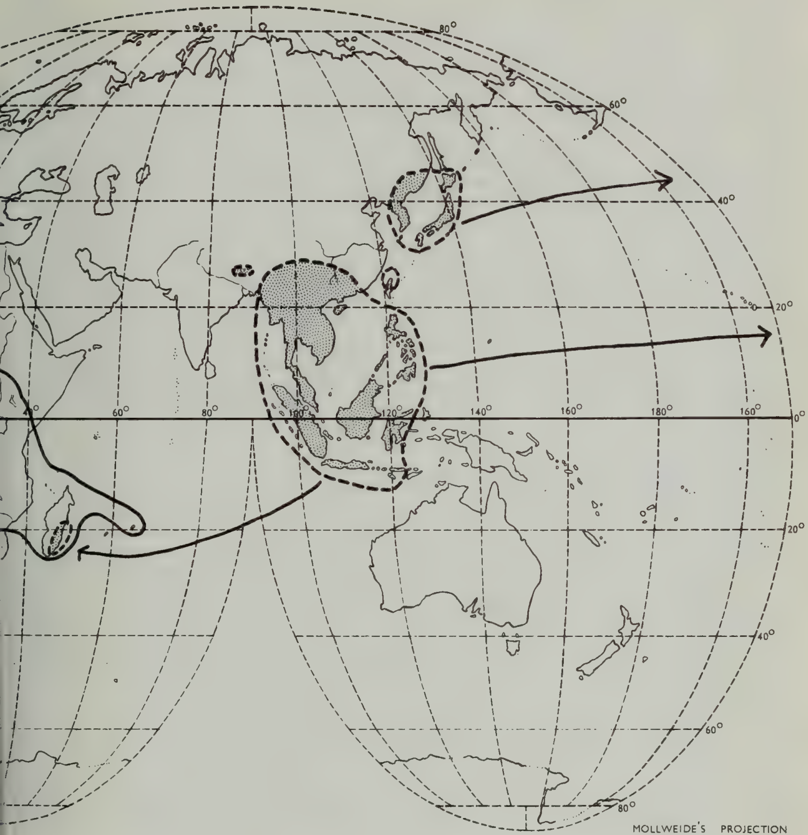
Fig. 59 Distribution of the Hypericoideae—Vismieae and Cratoxyleae: —— Vismieae, ▒ Cratoxyleae.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(Perrier de la Bâthie (1951) describes 26 species, all of which are said to be endemic.) The trends in the Vismieae are thus clearly from the New World to the Old (Fig. 59).

In the Cratoxyleae, the primary vicariance is between *Eliea* (Madagascar, monotypic) and *Cratoxylum* (Burma and south China to western Malesia, 6 species) (Gogelein, 1967; Robson 1972*a*, 1974). Neither genus is clearly more primitive than the other (cf. Baas, 1970), although the range of variation is much greater in *Cratoxylum*. The other two genera, which both show trans-Pacific links, seem to have been derived independently from *Cratoxylum*. One of these, *Thornea*, comprises two species of relict habitats in the Mexico-Guatemala border area (Breedlove & McClintock, 1976); the other, *Triadenum*, has one species (*T. breviflorum* (Wall. ex Dyer) Y. Kimura) in Assam (Khasia) and Taiwan, one species (*T. japonicum* Makino) in Japan, Korea and adjacent U.S.S.R., and two pairs of species—or two species each with two subspecies—in eastern U.S.A. and Canada (Robson, 1972*a* : fig. 2, 1976). Since the American species of *Triadenum* are, in general, more advanced than the Asian ones, an evolutionary trend eastward across the Pacific is apparent here also (Fig. 59).

The Hypericeae, as we have seen, comprise two genera, *Hypericum* and *Santomasia*, each of which has primitive characters not shared with the other. *Santomasia*, like *Thornea*, is confined to the Mexico-Guatemala border region; but its links are trans-Atlantic, not trans-Pacific, in that the primitive species of *Hypericum* (*H. bequaertii*, sect. 1. *Campylosporus*) is in tropical Africa. The primary vicariance in the Hypericeae is thus trans-Atlantic (Robson, 1977 : fig. 4, 1979 : table 2), and there is no clear directional indication from morphology.

In the Hypericoideae, therefore, the Vismieae show two separate trans-Atlantic trends from west to east, each of which continues to Madagascar (and one to Mauritius); the Cratoxyleae show a trans-Indian-Ocean vicariance followed by two separate trans-Pacific trends, one tropical and the other temperate; and the Hypericeae show an initial trans-Atlantic vicariance.

Distribution of *Hypericum*

(*a*) *Sect. 1.* Campylosporus *and its immediate derivatives*

Sect. 1. *Campylosporus*, which includes the most primitive species in *Hypericum*, is confined to tropical and southern Africa, south-western Arabia and nearby islands (Fernando Poo, Socotra, Grande Comore, Madagascar and Réunion) (Fig. 60; Robson, 1977 : figs 2, 4). Being confined to higher altitudes, the species all have restricted or more-or-less discontinuous distributions along the east African mountain chain from Eritrea to northern Cape Province (Bamps, 1971 : maps 72–76; Robson, 1979 : maps 1, 2). Two (*H. revolutum*, *H. roeperanum*) occur also in the Cameroon highlands, and one of these (*H. roeperanum*) has a wider western distribution, being found in Angola (Huila), Nigeria (Bauchi plateau) and Guinée (Fouta Djalon). Whilst such distribution patterns are typical of Afro-montane species (cf. Morton, 1972), a closer examination of the distributions of the various members of this section reveals several points of interest.

If the species of sect. *Campylosporus* are arranged in a relationship diagram (Figs 3, 61), it may be seen that the most primitive one (*H. bequaertii*) has a restricted (relict ?) distribution in the Ruwenzori Mountains. Its closest relative, *H. revolutum* subsp. *keniense*, also occurs on Ruwenzori but is found on the Virungas and the east African 'inselbergs' as well; and it, in turn, is incompletely distinct from the more advanced subsp. *revolutum*, which is widespread in Africa and occurs in Arabia.

The other taxa that appear to be directly related to subsp. *keniense* are all widely disjunct with the exception of *H. quartinianum*, which has probably spread into the area of subsp. *keniense* from much further north. Within sect. *Campylosporus* the disjunctions are to Socotra (*H. socotranum*) and Réunion (*H. lanceolatum* subsp. *angustifolium*), the latter being particularly similar morphologically to *H. revolutum* subsp. *keniense* (Robson, 1979). In addition, the two sections either confined to Central and South America (29. *Brathys*) or with the primitive species there (30. *Spachium*) appear to have direct relationships with *H. revolutum* subsp. *keniense*. The taxa directly derived from *H. bequaertii* and *H. revolutum* subsp. *keniense* thus comprise two on the other side of the Atlantic Ocean, two on islands noted for the occurrence of relict taxa, and two on the African mainland.

When these sections are associated with the relevant parts of sect. *Campylosporus* (Fig. 61), it can be seen that, in general, the taxa 'radiating' from *H. revolutum* subsp. *keniense* (in terms of morphology and other 'internal' characteristics) are distributed round its area in a similar 'radiating' fashion; and there is a second 'radiation' from the north of the area of sect. *Campylosporus* from the Ethiopia-Socotra region (Fig. 60).

The southern 'radiation' comprises five trends, which will be considered in an anticlockwise direction round the area of *H. revolutum* subsp. *keniense*:

(i) To the north-west, sect. 29. *Brathys* has its most primitive species (*H. styphelioides*) in Belize and Cuba.

(ii) To the south-west, sect. 30. *Spachium* has its most primitive species (*H. rigidum* = *H. meridionale* L. B. Sm.) in south-eastern Brazil (centred in Paraná).

(iii) To the south-east is *H. lanceolatum* (in Réunion and Grande Comore) with a derivative species, *H. madagascariense*, in north and central Madagascar and a derivative section, 26. *Humifusoideum*, of which the most primitive species (*H. sewense*) occurs in the Madang District of northern New Guinea (iii *a*).

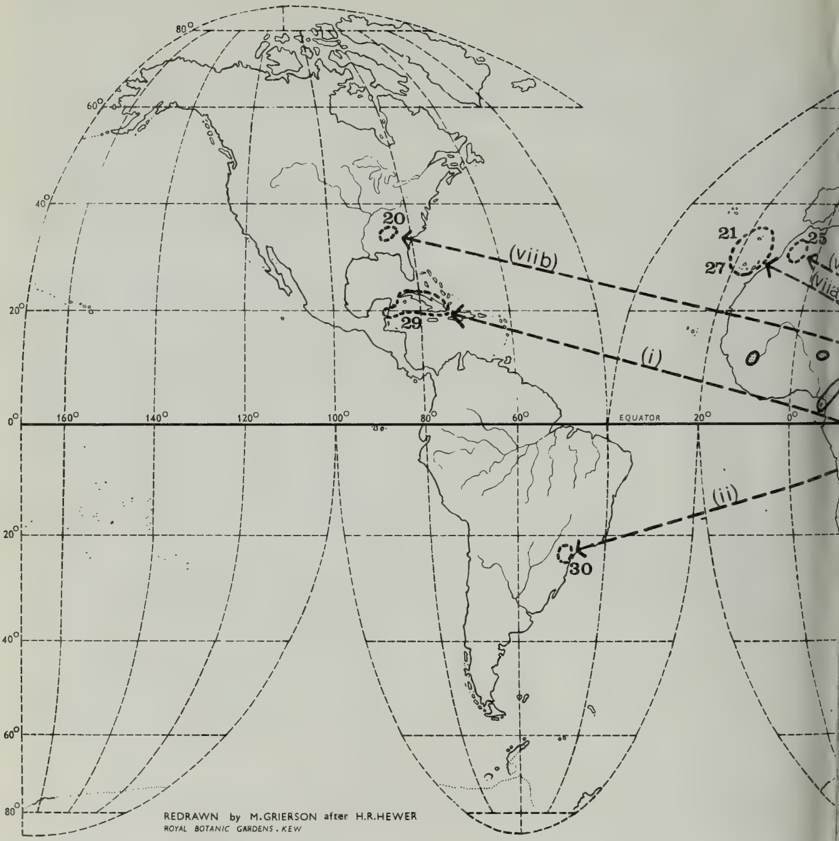
(iv) To the north-east, sect. 3. *Ascyreia*, which has its most primitive species (*H. mysurense*) in Sri Lanka and southern India, is in turn the source of the Eurasian and North American group that comprises sects 4–19.

(v) To the north-north-east (in Socotra) is *H. socotranum*, in which, I have included the plants that previous authors (e.g. Hutchinson, 1959 : 297) regarded as belonging to *H. mysurense*. *H. socotranum*, which comprises three taxa (subspecies ?), is in turn the most closely related species in sect. *Campylosporus* to three sections. Sect. 23. *Triadenioides* has its most primitive species (*H. scopulorum*) in Socotra itself (v *a*), whereas the most primitive form of the basic species of sect. 25. *Adenotrias* (*H. aegypticum*) is in southern Morocco. The monotypic sect. 24. *Heterophylla* (*H. heterophyllum*) from north-eastern Turkey is more advanced than some forms of *H. aegypticum* in all characters except for those of the flower, which lacks the specialised pollination syndrome of sect. *Adenotrias*. These two sections have therefore been treated as parts of a single 'radiation' from *H. socotranum* (v *b*).

The northern 'radiation' comprises the derivatives of two taxa, *H. revolutum* subsp. *revolutum* and *H. quartinianum*, both of which have quite wide distributions in Africa and also reach Arabia. They are not particularly closely related to each other (Fig. 61), but both appear to have given rise to distinct sections northward from the 'centre' of sect. *Campylosporus*:

(vi) *H. revolutum* subsp. *revolutum* is relatively constant in morphology throughout most of its wide range from Yemen south to Cape Province and west to Fernando Po, but in Ethiopia and Eritrea broader-leaved forms occur. The monotypic sect. 2. *Psorophytum* (*H. balearicum*), which is confined to the Balearic Islands (Fig. 70, p. 202), has apparently been derived from such broader-leaved forms by complete separation of the styles, reduction of the inner floral whorls to tetramery, and enlargement of the pellucid glands (vi *a*). For trend vi *b* see footnote on p. 187.

(vii) *H. quartinianum* has a smaller range than *H. revolutum*, scarcely penetrating southward beyond Tanzania; but it seems to have been a fertile source of derivative groups. In this trend there is a tendency for the styles to become completely united or at least appressed; and in *H. quartinianum* and the more specialised *H. roeperanum* this condition is sometimes achieved. The latter species has the widest distribution in sect. *Campylosporus*, not only extending from Ethiopia to the Transvaal, but occurring disjunctly in Cameroon, Niger, Guinée and Angola. The complete union of styles is constant in *H. synstylum*, a local species of eastern Ethiopia and Somalia, which is the nearest relative of *H. frondosum*, the most primitive species in the north American sect. 20. *Myriandra* (vii *b*). Here the styles are also completely united, at least during flowering.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REDRAWN by M.GRIERSON after H.R.HEWER
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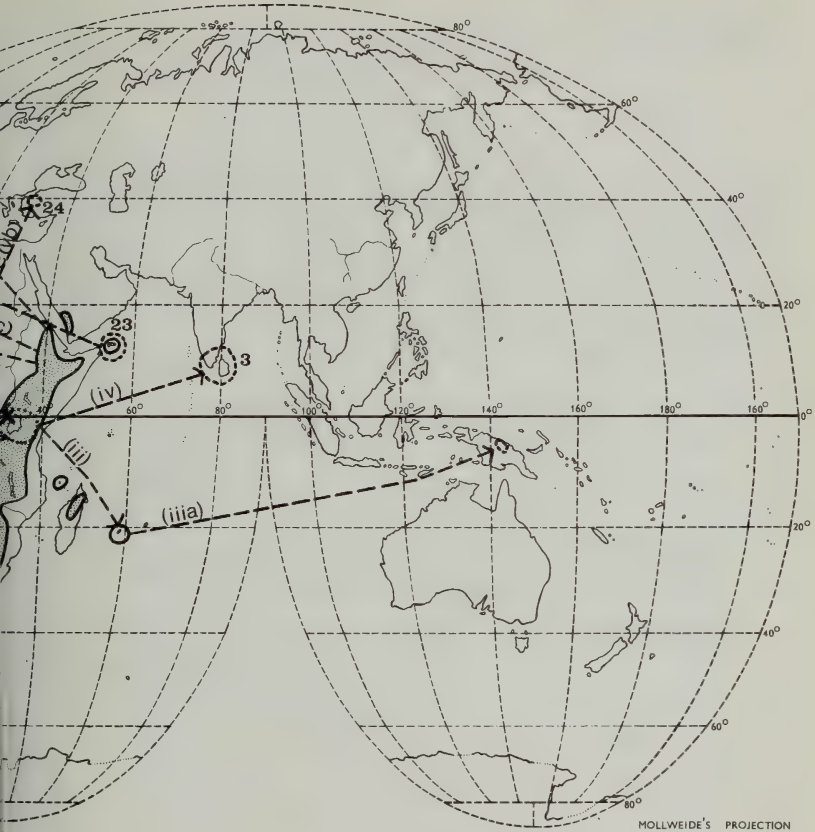
Fig. 60 Distribution of sect. 1. *Campylosporus* and of the most primitive members of sections directly related to it. Arabic numerals indicate sections; Roman numerals indicate trends (see Fig. 61 and footnote, p. 187). •••• = area of distribution of *H. revolutum* subsp. *keniense.* x = area of *H. bequaertii.*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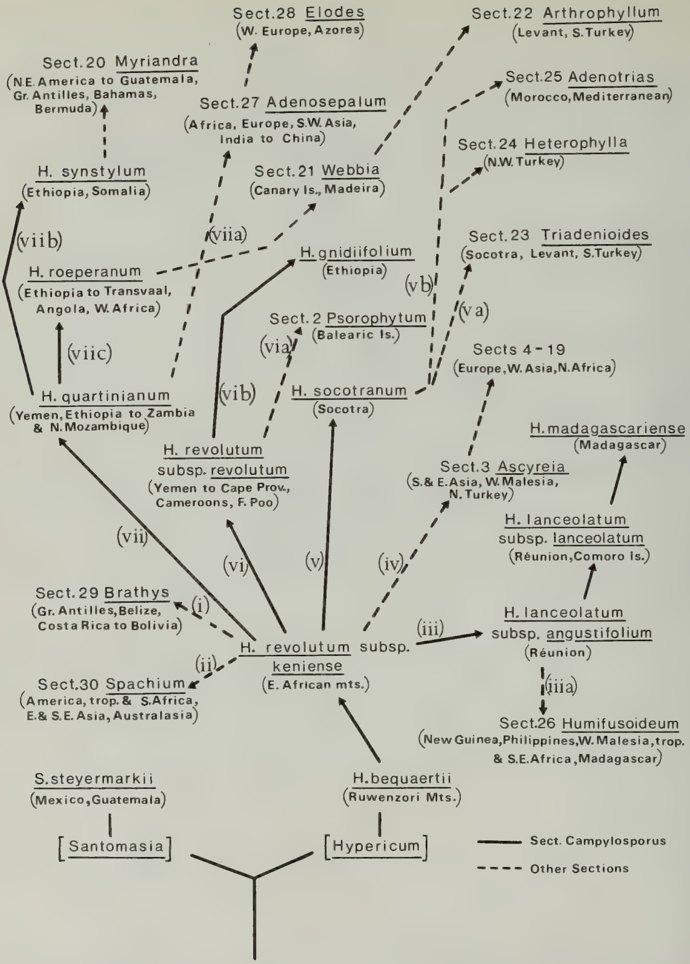
Sect.28 Elodes
(W. Europe, Azores)
Sect.22 Arthrophyllum
(Levant, S.Turkey)
Sect.20 Myriandra
(N.E. America to Guatemala, Gr. Antilles, Bahamas, Bermuda)
Sect.25 Adenotrias
(Morocco, Mediterranean)
Sect.27 Adenosepalum
(Africa, Europe, S.W. Asia, India to China)
Sect.24 Heterophylla
(N.W. Turkey)
H. synstylum
(Ethiopia, Somalia)
Sect.21 Webbia
(Canary Is., Madeira)
(viib)
(viia)
Sect.23 Triadenioides
(Socotra, Levant, S.Turkey)
H. gnidiifolium
(Ethiopia)
H. roeperanum
(Ethiopia to Transvaal, Angola, W. Africa)
(vb)
(va)
Sect. 2 Psorophytum
(Balearic Is.)
(via)
(viic)
Sects 4-19
(Europe, W. Asia, N. Africa)
(vib)
H. socotranum
(Socotra)
H. quartinianum
(Yemen, Ethiopia to Zambia & N. Mozambique)
H. madagascariense
(Madagascar)
H. revolutum subsp. revolutum
(Yemen to Cape Prov., Cameroons, F. Poo)
Sect.3 Ascyreia
(S.& E. Asia, W. Malesia, N. Turkey)
H. lanceolatum subsp. lanceolatum
(Réunion, Comoro Is.)
(vii)
(vi)
(v)
(iv)
Sect.29 Brathys
(Gr. Antilles, Belize, Costa Rica to Bolivia)
(i)
(iii)
H. lanceolatum subsp. angustifolium
(Réunion)
H. revolutum subsp. keniense
(E. African mts.)
(ii)
Sect.30 Spachium
(America, trop. & S. Africa, E.& S.E. Asia, Australasia)
(iiia)
Sect.26 Humifusoideum
(New Guinea, Philippines, W. Malesia, trop. & S.E. Africa, Madagascar)
S. steyermarkii
(Mexico, Guatemala)
H. bequaertii
(Ruwenzori Mts.)
[Santomasia]
[Hypericum]
Sect. Campylosporus
Other Sections

Fig. 61 Relationships diagram of the species in sect. 1. *Campylosporus*, showing their distributions and their connections with other sections (cf. Fig. 3). Roman numerals indicate trends discussed in the text (but see footnote, opposite).

In the other group related to *H. quartinianum* (sects 27. *Adenosepalum* and 28. *Elodes*), however, the styles are separate. The two most primitive species of sect. 27 (*H. glandulosum* and *H. reflexum*) are both natives of the Canary Islands and Madeira.

H. roeperanum, also, has given rise to groups with partly or wholly free styles. In *H. gnidiifolium*, a localised Ethiopian endemic, they are free only near the apex; but in the monotypic sect. 21. *Webbia* (*H. canariense*), from the Canary Islands and Madeira, they are completely free and separate at the base, and the inner floral whorls are trimerous.* From it is derived the eastern Mediterranean group of dwarf shrubs comprising sect. 22. *Arthrophyllum*.

(*b*) *Sect. 3.* Ascyreia *and its derivatives. I. Sects 3–8* (Fig. 62)

Sect. 3. *Ascyreia* has its most primitive species, *Hypericum mysurense*, in the extreme south of its range, in Sri Lanka and south India, and immediate derivatives in Orissa (*H. gaitii*) and Nepal (*H. podocarpoides* N. Robson, *H. cordifolium*) (Robson 1977*b*). From Nepal, the distribution of the section is effectively continuous westward to the Afghanistan border (*H. oblongifolium*) and eastwards to lowland China and northern Taiwan (*H. monogynum*). There are also two disjunct areas: (i) in north-western Turkey and adjacent Bulgaria is *H. calycinum*, which is most closely related to the western Himalayan *H. oblongifolium*, and in Indonesia, from Sumatra to Flores and south-western Celebes, are *H. leschenaultii* and (in north Sumatra only) *H. uralum*. The latter also occurs in the central to eastern Himalaya, whilst *H. leschenaultii* is most closely allied to an undescribed species from northern Thailand.

Sect. 4. *Takasagoya* comprises four species, which are confined to Taiwan except for *H. geminiflorum*, which reaches northern Luzon. The most primitive species, *H. formosanum*, is most closely related to *H. monogynum*, but to the Szechwan form, not the one that occurs on Taiwan itself.

Sect. 5. *Androsaemum* also comprises four species, of which the most primitive is *H. grandifolium* of the Canary Islands and Madeira. Its nearest relative in sect. *Ascyreia* is *H. griffithii*, which is endemic to Bhutan. The large gap between the Canary Islands and Bhutan is to some extent bridged by two of the other species, *H. hircinum* and *H. androsaemum*, which have dissected distributions from western Europe and adjacent Africa to northern Iran. *H. hircinum*, which in general is the more southern, has also been found in south-western Saudi Arabia (Asir).

The monotypic sect. 6. *Inodora* (*H. xylosteifolium*) is confined to the high-rainfall area of Georgia and adjacent Turkey. Like sect. *Androsaemum*, its nearest relative is the central Himalayan *H. griffithii*.

Sect. 7. *Roscyna* has four species, of which three occur only in central and western China. The most primitive, *H. elatoides*, is most closely related to *H. monogynum* and is confined to southern Shensi; *H. pedunculatum* occurs in Shensi and Hupeh; and *H. przewalskii* is spread more widely, from Shensi westward to Tsinghai and south to Yunnan. The fourth species, *H. ascyron*, is very variable, but it does not seem possible to recognise any subspecies or segregates such as *H. gebleri* Ledeb. It stands apart morphologically from the other three species and has much the widest distribution of the four. In eastern Asia it occurs from Yunnan and northern Vietnam northward to Manchuria and westward along the mountains skirting Mongolia to the Altai Mts and north-eastern Kazakhstan, including southern

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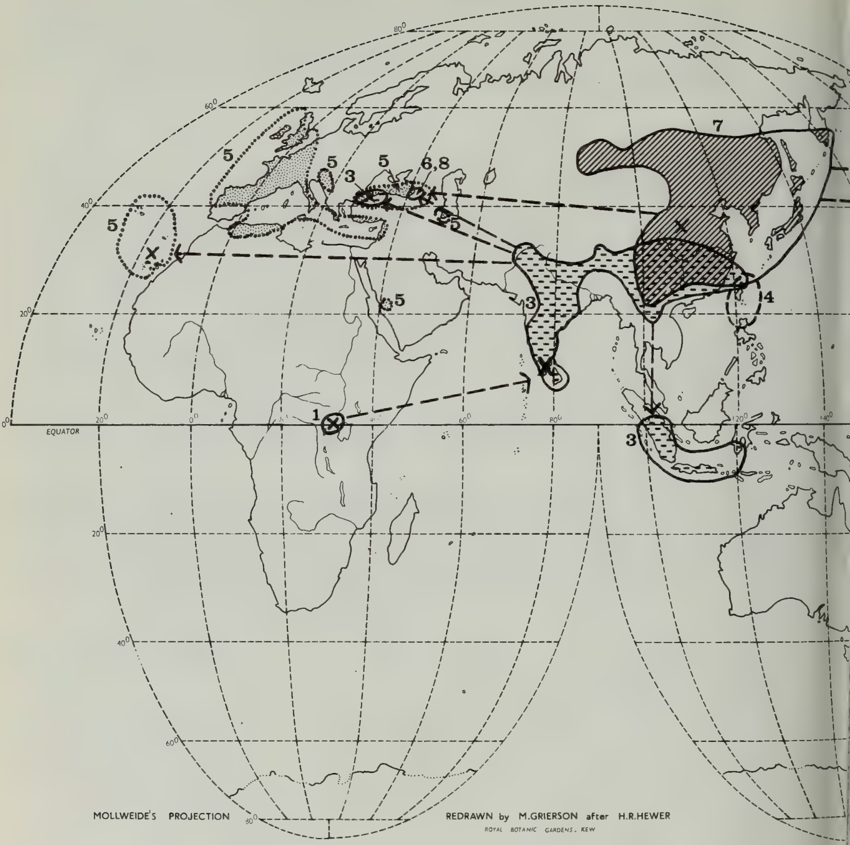
*At a late stage in the preparation of this paper, I realised that *H. gnidiifolium* was derived from *H. roeperanum*, not *H. revolutum*. Its markedly discolorous, densely reticulate-veined leaves and 3–5-flowered inflorescences are consistent with this hypothesis; and its incompletely united styles can be interpreted as an intermediate stage between the usually completely united styles of *H. roeperanum* and the free ones of *H. canariense* (sect. 21. *Webbia*). *H. gnidiifolium* thus belongs to trend vii c, not vi b as shown in Fig. 61. In making this alteration, which does not affect any of the phytogeographical argument, I am agreeing in part with Moggi & Pisacchi (1967); but, unlike these authors, I prefer to retain *H. gnidiifolium* as a species distinct from *H. roeperanum*.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MOLLWEIDE'S PROJECTION
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ROYAL BOTANIC GARDENS, KEW

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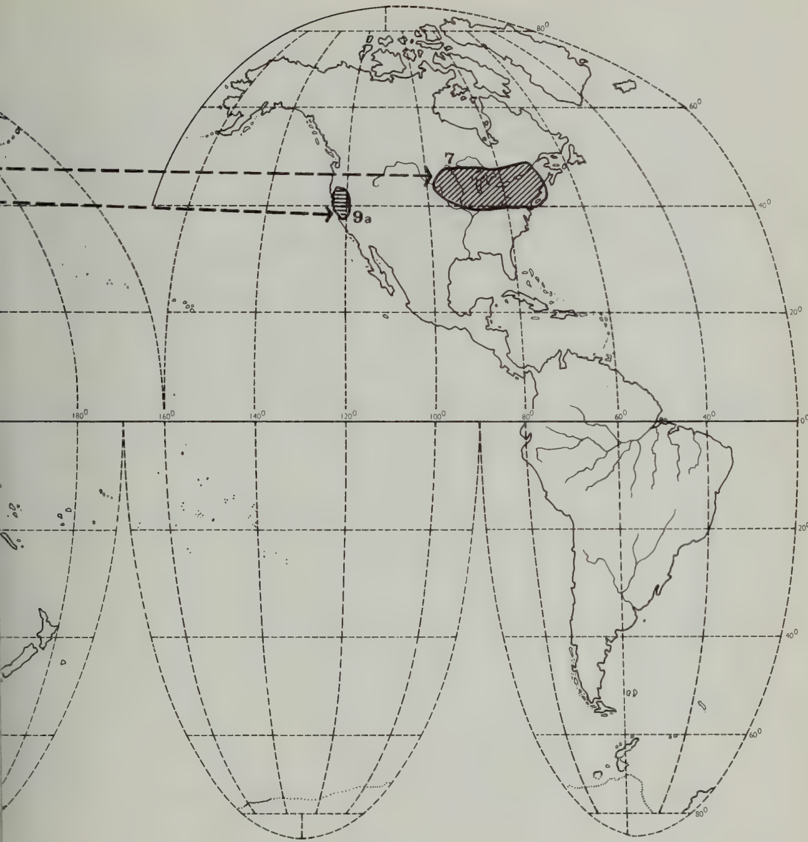
Fig. 62 Distribution of sect. 3. *Ascyreia* and four of its immediately derivative sections: 4. *Takasagoya, 5. Androsaemum*, 6. *Inodora* and 7. *Roscyna.* ⊗ = centre of distribution of sect. 1. *Campylosporus*; x = areas of most primitive species of sects 3, 5 and 7.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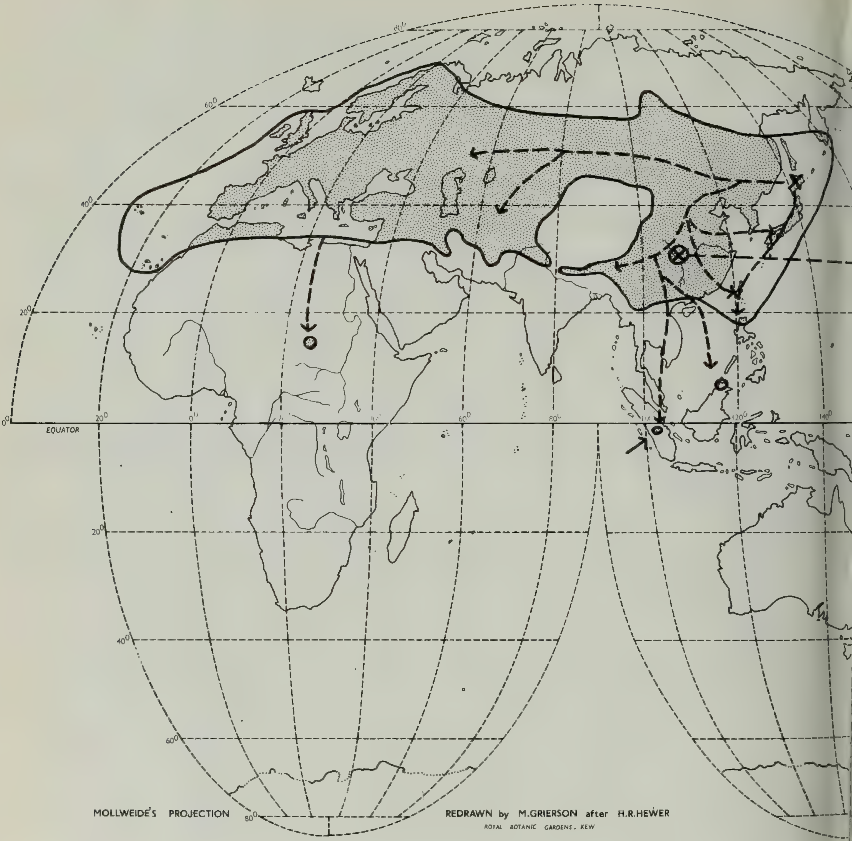
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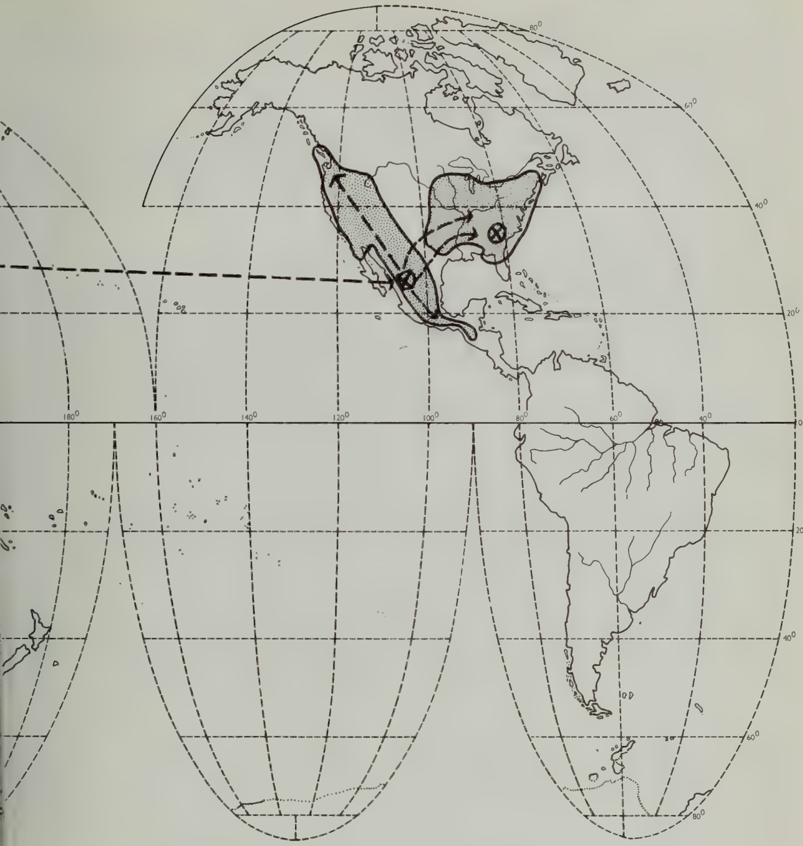
Fig. 63 Distribution of sect. 9. *Hypericum*. ⊗ (China) = area of *H. pedunculatum* (sect. 7); ⊗(Mexico) = centre of area of *H. formosum*; ⊗(eastern U.S.A.) = area of *H. graveolens*.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Kamchatka, Sakhalin, Japan and Taiwan (one record). It also occurs in the north-eastern part of the U.S.A. and adjacent Canada. The American form, with pyramidal branching (*H. pyramidatum* Aiton), can be matched in different parts of the Asian range (e.g. Yunnan, Japan).

As well as being the origin of the large sect. 9. *Hypericum* (see p. 190, Fig. 63), sect. 7. *Roscyna* has apparently given rise to two monotypic sections. Of these, sect. 8. *Bupleuroides* (*H. bupleuroides*) is related to *H. pedunculatum* and *H. przewalskii* but is separated from them by the central Asian plateau and steppe region. It occupies almost the same area of western Transcaucasia as does sect. 6. *Inodora*.

The other species, *H. concinnum*, which was included in sect. *Hypericum* in Part I (Robson, 1977*a*), is the only member of Sect. 9a. *Concinna* (see p. 173). It is confined to the coastal range and Sierra Nevada of California from the San Francisco region northwards, and thus, like American *H. ascyron* itself, is separated from its relatives by the north Pacific Ocean.

(*c*) *Sect. 3.* Ascyreia *and its derivatives. II. Sect. 9* (Fig. 63)

The major derivative of sect. 7. *Roscyna* is sect. 9. *Hypericum*, a large section with a wide north-temperate distribution. Like sect. *Roscyna* it has its most primitive species in eastern Asia or, at least, centred there, and all members could be derived from a plant resembling *H. pedunculatum* (sect. *Roscyna*, from Hupeh). It is not possible to nominate one species as the most primitive. *H. yamamotoi* (from Hokkaido, Japan) most nearly resembles an ancestral species in some respects. It is related to (i) an east Asian group (Kamchatka to Luzon, northern Vietnam and central Nepal, with outliers in Sumatra and Borneo) and (ii) a mainly west Asian and European group (*H. maculatum*, from Siberia to western Europe, and its derivatives; *H. attenuatum*, from north China and adjacent Siberia, and *H. elegans*, from central Siberia to central Europe; *H. perforatum*, which looks and behaves like the result of an allopolyploid cross between *H. maculatum* and *H. attenuatum*). (iii) In addition, there is a North American group, which comprises two subgroups: *H. formosum*, in northern and central Mexico, and its derivatives in Mexico, the U.S.A. and adjacent Canada (*H. scouleri*, *H. punctatum*, *H. pseudomaculatum*) and the *H. oaxacanum* affinity, mainly in central and southern Mexico and adjacent Guatemala. The most primitive species in the latter subgroup, which occurs from southern Vera Cruz to Guatemala and is close to *H. oaxacanum*, is as yet unnamed. It has another very close relative, however, in North Carolina, *H. graveolens*, which appears to have hybridised with a species from the other subgroup, *H. punctatum* (see p. 167). Although neither *H. formosum* nor *H.* sp. aff. *oaxacanum* can be regarded as wholly primitive in the North American group, a plant possessing the primitive characters of both species would be very near *H. pedunculatum* and *H. yamamotoi* from eastern Asia.

(*d*) *Sect. 3.* Ascyreia *and its derivatives. III. Sects 10–16* (Fig. 64)

The most primitive section of the *Olympia* group (sects 10–16), from which all the others have apparently been derived, is sect. 10. *Olympia*, which has two disjunct areas: i) *Hypericum olympicum* p.p. in Greece, adjacent Yugoslavia and Bulgaria, north-western Turkey and some northern Aegean islands; ii) *H. olympicum* p.p. and *H. polyphyllum* in southern Turkey from Antalya to the Amanus Mountains (Robson, 1980*b*). The most primitive member of the section, *H. polyphyllum* subsp. *lycium* Robson & Hub.-Mor., which is confined to a small area near Takhtali Dag in south-western Antalya, has its nearest ancestral relatives in Nepal (*H. cordifolium* and *H. podocarpoides* N. Robson, sect. 3. *Ascyreia*).

Sect. *Olympia* has given rise to two groups, one eastern (sect. 12. *Origanifolia* in Turkey and western Transcaucasia, with the derivative sect. 11. *Campylopus* extending north-westwards into Greece and Bulgaria) and the other primarily north-western (sect. 13. *Drosocarpium*). Sect. *Drosocarpium* has its most primitive species (*H. rumeliacum*) centred

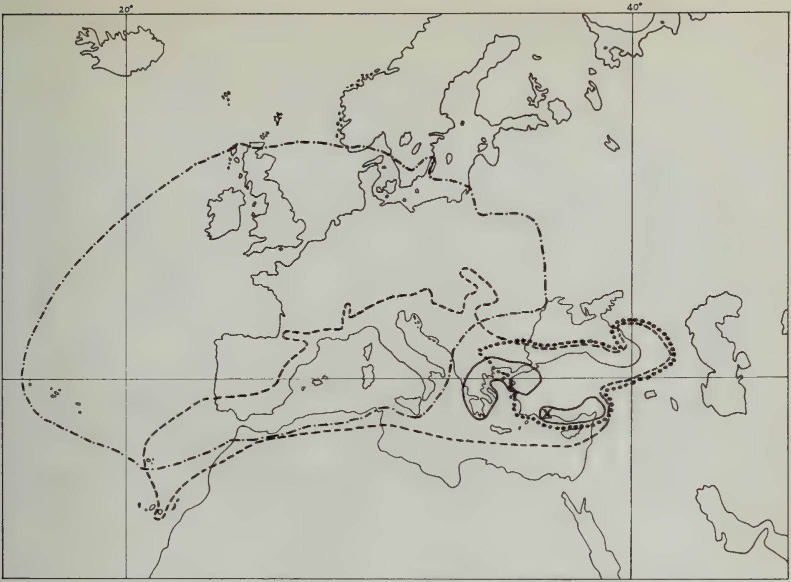

Fig. 64 Distribution of *Olympia* group (sects 10–16); ▬ sect. 10. *Olympia*, •••• sects 11, 12, 15, 16; ‒ ‒ sect. 13. *Drosocarpium*; ‒•‒ sect. 14. *Oligostema*. x = area of most primitive taxon of sect. 10—*H. polyphyllum* subsp. *lycium*.

in the southern Balkan peninsula (Makhedonia, Thrace), and extends eastward into Transcaucasia (*H. bithynicum*, *H. montbretii*), southward into Crete (*H. trichocaulon*, *H. kelleri*) and Cyprus (*H. repens**), westward throughout the Mediterranean and north-west Africa to Madeira and the Canary Islands (*H. perfoliatum*) and northward to the Balkan mountains, Carpathians, Alps and Pyrenees (*H. richeri* sens. lat.).

Sect. *Drosocarpium*, in turn, has given rise to three sections: Sect. 14. *Oligostema* (in the western Mediterranean, Madeira and the Azores, with *H. linarifolium* also in Atlantic Europe and *H. humifusum* extending to northern Scotland, southern Scandinavia, western U.S.S.R. and the northern Balkans), sect. 15. *Thasia* (*H. thasium* in Thasos and the adjacent mainland) and sect. 16. *Crossophyllum* (*H. adenotrichum* in western Anatolia, *H. orientale* in northern Anatolia and adjacent Transcaucasia).

(*e*) *Sect. 3.* Ascyreia *and its derivatives. IV. Sects 17–19* (Figs 65, 66)

This second western Eurasian group (the '*Hirtella*' group) seems to have been derived from the same part of sect. 3. *Ascyreia* as has the *Olympia* group, viz. the Nepalese *Hypericum cordifolium* and *H. podocarpoides*. However, whereas the *Olympia* group (with basic chromosome numbers n = 9–7) is centred in western Anatolia and has primitive species

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**H. aucheri* and *H. repens* were included in sect. 14. *Oligostema* in Part I (Robson, 1977*a*; also in Robson, 1968*b*) on account of their vittate capsules; but their other characters all indicate that their affinities are clearly with sect. 13. *Drosocarpium* (with *H. rumeliaacum* and *H. trichocaulon*, respectively), to which they must therefore be transferred.

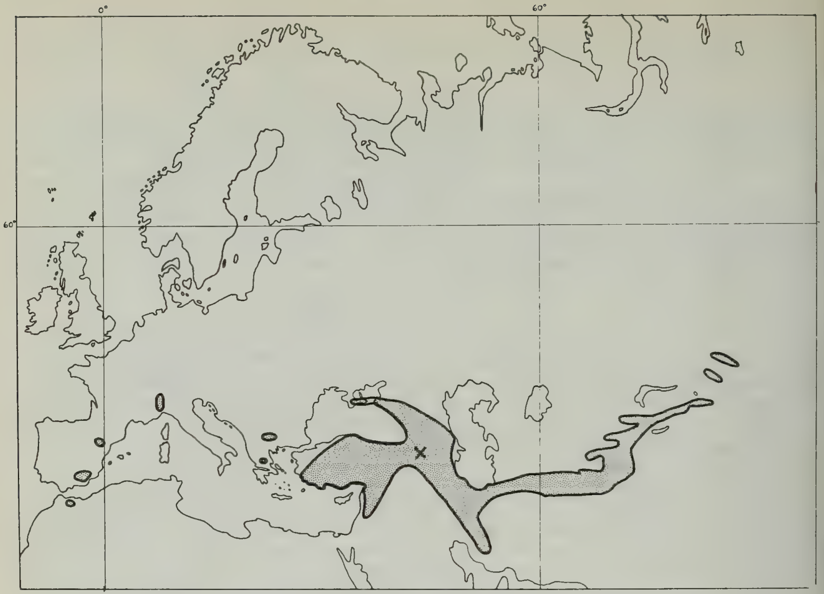

Fig. 65 Distribution of sect. 17. *Hirtella*. x = area of most primitive species.

which are morphologically closer to *H. podocarpoides*, the *Hirtella* group (with basic chromosome numbers probably n = 10–8) is centred in eastern Anatolia and Transcaucasia and has primitive species which are morphologically closer to *H. cordifolium*.

From eastern Anatolia, species of sect. 17. *Hirtella* (Fig. 65) extend round the Fertile Crescent south-westward to Israel and Jordan and south-eastward along the Zagros Mountains to Shiraz in Iran. Of the four species that occur farther east than Khrebet Dag (U.S.S.R.-Turkmenia), two (*H. elongatum* and *H. scabrum*) reach the Altai Mts (U.S.S.R.-Kazakhstan). Beyond the Caucasus-Anatolian region, where by far the greatest number of species are found, the section 'peters out' westwards with two markedly disjunct species which have distributional 'arcs' to the south and north, respectively, of Italy. To the south, the mainly Central Asian to Anatolian *H. elongatum* occurs in central Greece (as *H. tymphresteum* Boiss. & Spruner) as well as in Morocco and south-eastern Spain (as *H. callithyrsum* Cosson). This species has also been recorded from the Crimea, as has *H. hyssopifolium*; but all the specimens from there that I have seen belong to *H. lydium* (= *H. ponticum* Lipsky). To the north, *H. hyssopifolium* sens. str., which approaches the primitive species of sect. 19. *Coridium* (*H. asperulifolium*), is found in the central Balkans (Serbia, Bulgaria), the south-western Alps (France, Italy) and eastern and south-eastern Spain, where it meets *H. elongatum*.

Sect. 19. *Coridium* (Fig. 66) comprises five species, four of which are morphologically and geographically isolated. Of these, three form a morphological and geographical series: *H. asperulifolium* (eastern Transcaucasia), *H. coris* (central and western Alps) and *H. ericoides* (south-eastern Spain, Morocco, Tunisia). The other two are closely inter-related but more

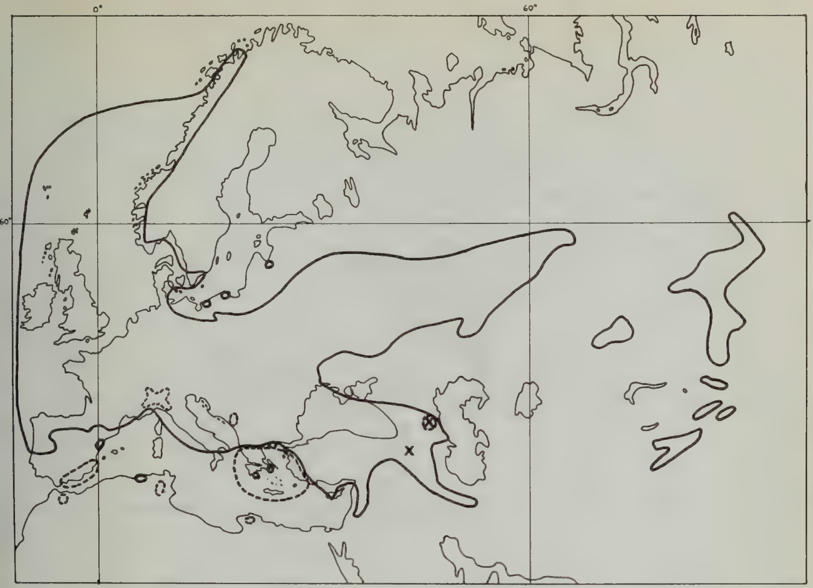

Fig. 66 Distribution of sects 18. *Taeniocarpium* —— and 19. *Coridum* - - - *x* = area of most primitive species in sect. 18, ⊗ = area of most primitive species in sect. 19 (*H. asperulifolium*).

distantly related to the first three: *H. empetrifolium* (N. Albania, Aegean region, Cyrenaica) and *H. amblycalyx* (Crete). The recently described Cretan *H. jovis* Greuter is very similar to the latter and may be conspecific with it.

The other section in the *Hirtella* group, sect. 18. *Taeniocarpium* (Fig. 66), has the most primitive form of its most primitive species, *H. linarioides* (i.e. that named *H. polygonifolium* Rupr.), in Transcaucasia. Thence the section extends round the Fertile Crescent south-westward to Israel (Mt Carmel) and eastward to the Elburz Mts. It is present throughout Anatolia except the extreme west; but, apart from two widespread species, it is otherwise confined to isolated areas round the north of the Mediterranean and Black Sea: in Greece (*H. taygeteum*—Taiyetos Mts; *H. fragile*—Attica, Evvoia), the central Balkans and the Crimea (*H. linarioides*), Albania (*H. haplophylloides*), and the Pyrenees and western Alps (*H. nummularium*). One of the two widespread species, *H. hirsutum*, has a mainly 'continental' distribution, from northern Iran westward to Algeria, Spain and eastern Ireland, and northward to beyond the Arctic Circle in Norway and eastward to central Siberia (R. Yenisei valley). The other, *H. pulchrum*, has an 'Atlantic', north-west European distribution, from northern Portugal to eastern Germany, southern Norway and the Faröes, with scattered localities further east.

(*f*) *Sect. 20.* Myriandra (Fig. 67)

The most primitive species in sect. 20. *Myriandra*, *Hypericum frondosum*, is restricted to a relatively small area in south-eastern U.S.A. around the Cumberland Mountains (east and

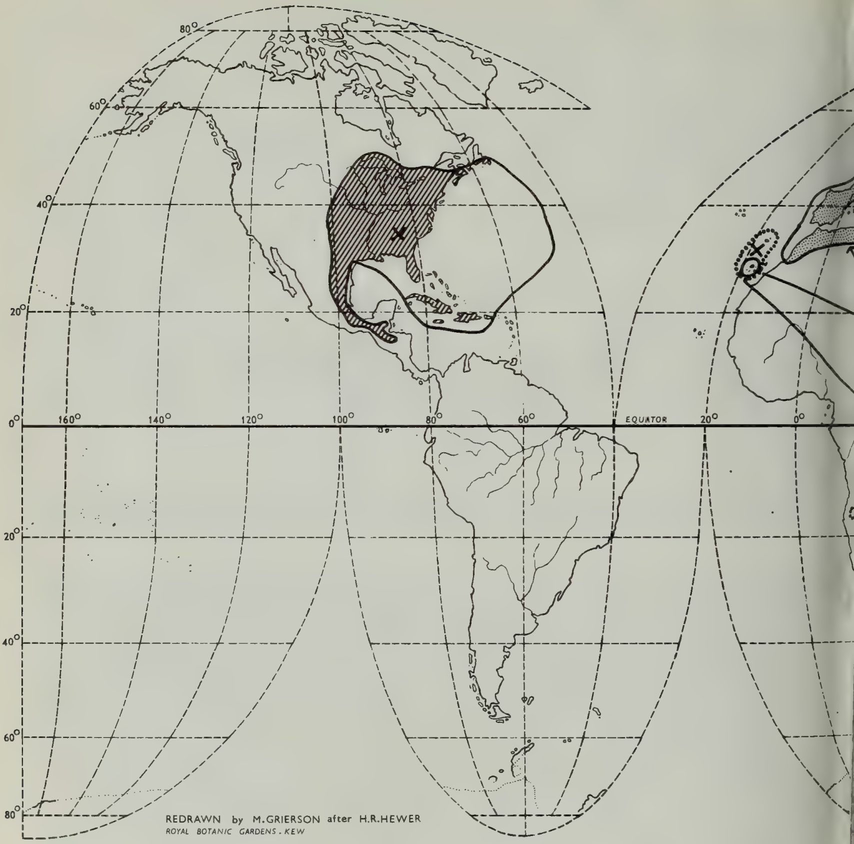
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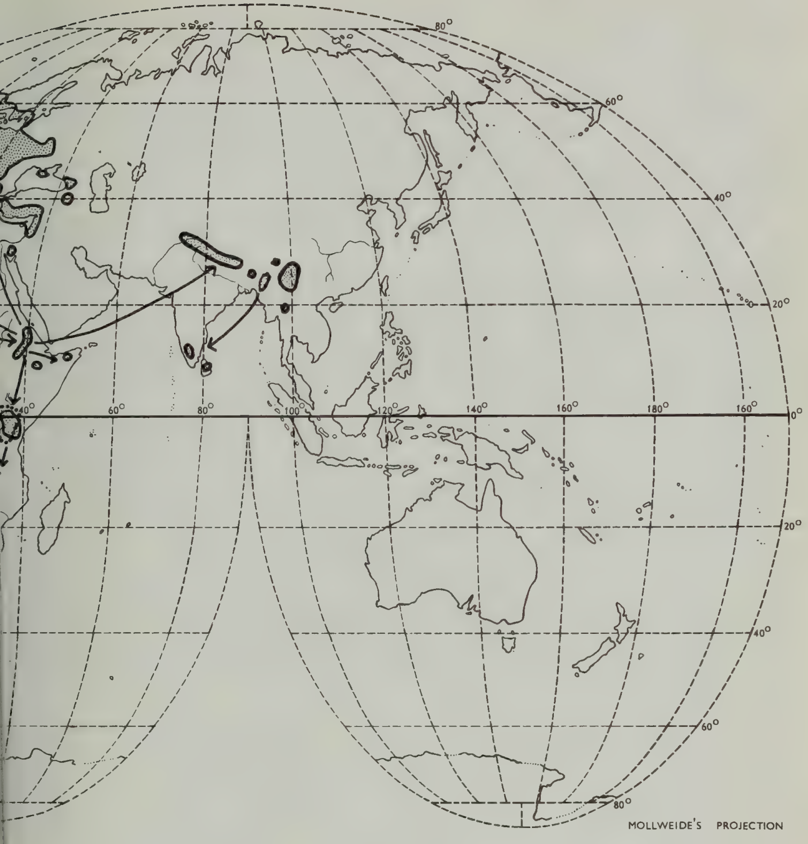
Fig. 67 Distribution of sects 20. *Myriandra* ▨ and 27. *Adenosepalum:* ••• *H. glandulosum* group, ▨ *H. reflexum* group. x = areas of most primitive species.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central Tennessee, central and south-western Georgia and northern Alabama). In its meristic variation it foreshadows two of the major trends which the section displays, viz. pentamerous ('*Hypericum* proper') and tetramerous ('*Ascyrum*') perianth whorls (Figs 4, 5). The '*Ascyrum*' group is more south-eastern in distribution, with only *H. crux-andreae* (*H. stans*)* occurring as far north as New Jersey; the area of one of the mainly Florida species (*H. tetrapetalum*) extends into Cuba, whilst only *H. hypericoides* subsp. *hypericoides* occurs south and east of Texas (Mexico to Honduras Republic) as well as in Bermuda, the Bahamas and the Greater Antilles. Of the essentially pentamerous species, the '*Myrtifolium*' group (which includes the tetramerous *H. microsepalum*—Fig. 5) is wholly North American, with the area of *H. ellipticum* extending north to Lake Superior and Newfoundland. The other pentamerous 'branch' in Fig. 5 comprises the central to northern '*Prolificum*' group, which has given rise to a more southern, narrow-leaved series, the '*Galioides*' group. The latter is centred in the south-eastern U.S.A., with *H. nitidum* occurring also in Cuba and Belize (but not Mexico) and giving rise in Cuba to *H. limosum* Griseb.

(*g*) *The Macaronesian and north-east African links with the Mediterranean (Sects 2, 21–25)* (Figs 68–70)

Sect. 21. *Webbia*, in my view, comprises one variable species, *Hypericum canariense*, which occurs both in the Canary Islands (all except Fuerteventura and Lanzarote) and in Madeira (Fig. 69). Its nearest ancestral form is to be found among the representatives of *H. roeperanum* and *H. gnidiifolium* in Ethiopia, and it, in turn, appears to be ancestral to a group of five species in the Levant and southern Turkey (sect. 22. *Arthrophyllum*) (Fig. 69). *H. balearicum* (sect. 2. *Psorophytum*) seems to be related directly to the north-east African complex of *H. revolutum* (Fig. 70).

The island of Socotra is rich in endemic *Hypericum* species, which form a morphological link between the east tropical African *H. revolutum* subsp. *keniense* (sect. 1. *Campylosporus*) and several Mediterranean species. The *H. socotranum* group itself is very variable and consists of three distinct entities (species or subspecies) in Socotra. Also on this island and related to one member of the *H. socotranum* group are the primitive members of sect. 23. *Triadenioides*, three species in all, which are clearly closely allied to two species from southern Turkey and the Levant, *H. ternatum* and *H. pallens* (Fig. 68).

H. socotranum sensu stricto is the nearest relative of two other mainly Mediterranean sections, sects 24. *Heterophylla* and 25. *Adenotrias*. The monotypic sect. *Heterophylla* (*H. heterophyllum*) is confined to a small region of western Anatolia, whereas the members of sect. *Adenotrias* occur in scattered areas over the Mediterranean and north Africa, mostly on islands (Figs 68, 69). The most primitive forms of *H. aegypticum* are found in southern Morocco, and the forms become progressively more reduced in an eastward direction. The other two species are in the east, *H. russeggeri* in Syria and southern Turkey, *H. aciferum* in Crete (Figs 68, 69).

In view of this prevailing eastward trend, it seems possible (though unlikely) that *H. heterophyllum* has been derived from *H. aegypticum*, i.e. that it has reverted to homostyly rather than that their ancestral lines diverged before the evolution of heterostyly.

(*h*) *Old-World transcontinental distributions I. Sect. 26.* Humifusoideum (Figs 7, 70)

The distribution of sect. 26. *Humifusoideum* provides a considerable interpretation problem. The most primitive species, *Hypericum sewense*, has been collected only once, from Madang District in north-eastern New Guinea; but the other four species of this section in New Guinea are closely related to it. The group most closely related to these species, however, comprises the Madagascar-Mascarene members of sect. 1. *Campylosporus*, of which *H. lanceolatum* subsp. *angustifolium* is most similar morphologically to *H. sewense* (Figs 3, 60, 61).

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*For an explanation of this synonymy, see Robson (1980*c*).

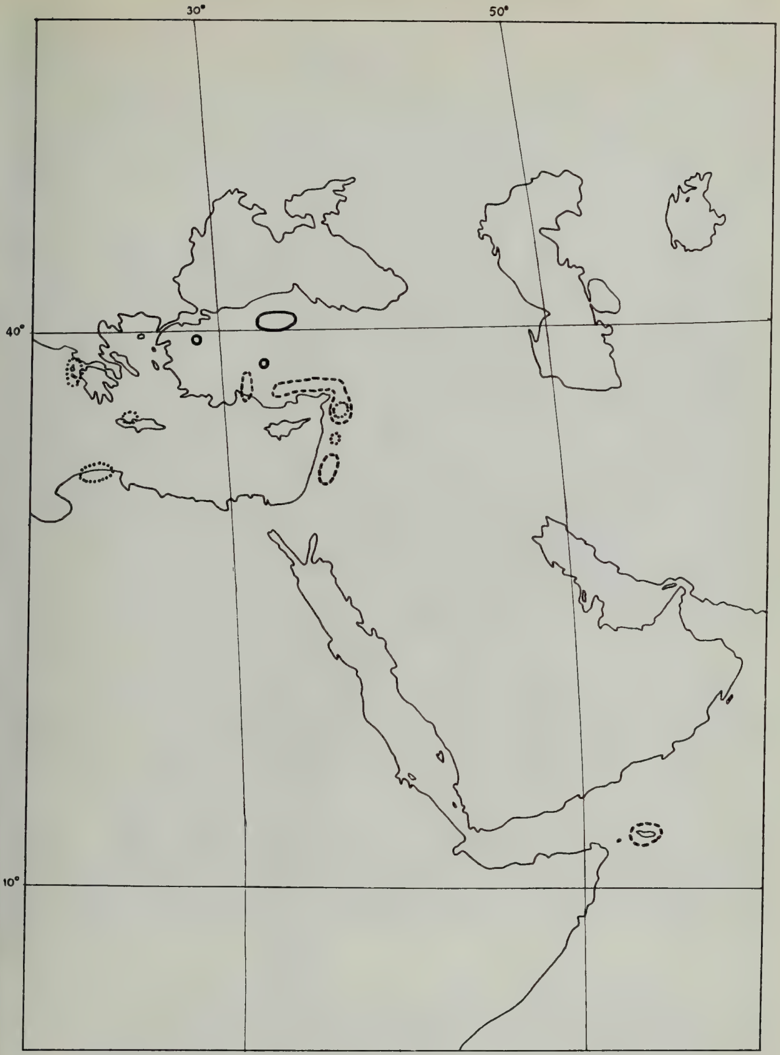


Fig. 68 Distribution of sects 23. *Triadenioides* ▬ ▬ 24. *Heterophylla* —— and 25. *Adenotrias* (excluding *H. aegypticum* in part) •••• .

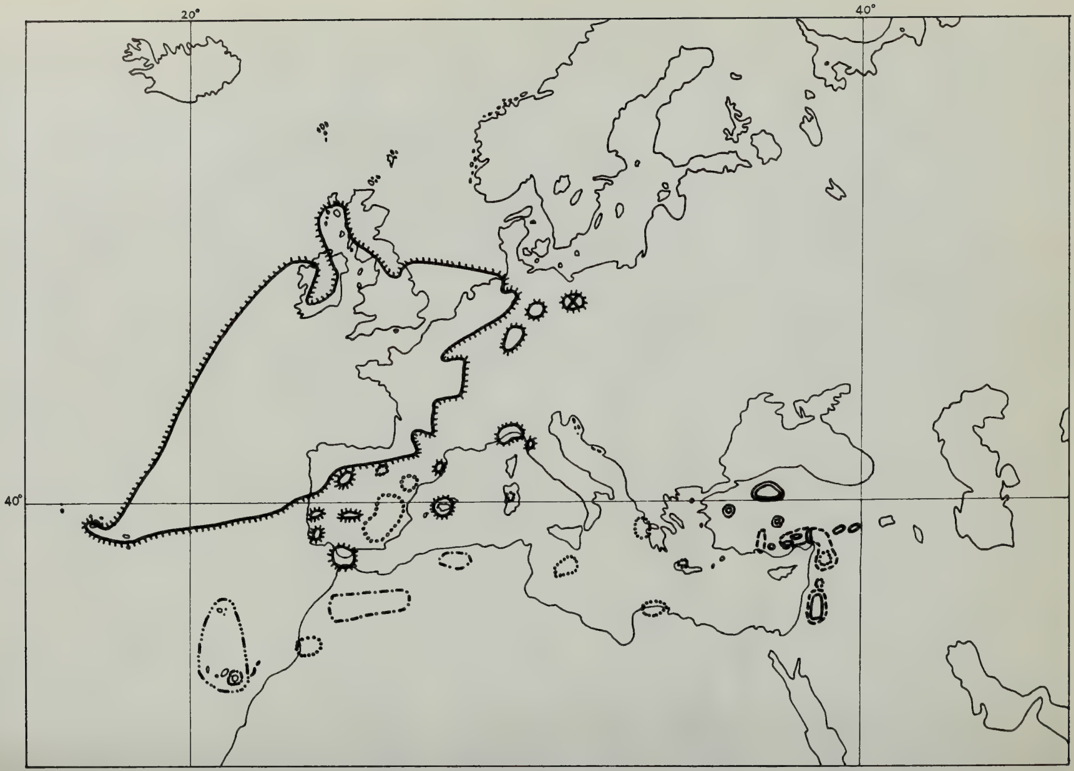


Fig. 69 Distribution of sects 21. *Webbia* -·-·-, 22. *Arthrophyllum* ▬, 23. *Triadenioides* - - -, 24. *Heterophylla* ═ , 25. *Adenotrias* (all species) ••• , 27. *Adenosepalum* (*H. coadunatum* -·-· and *H. caprifolium* ∘∘∘ only) and 28. *Elodes* ▥. x = extinct.

The derivative species of the New Guinea 'core' of the section are in three widely scattered groups: (i) *H. pulogense* in northern Luzon (Philippine Is.), (ii) *H. beccarii*, with two subspecies respectively in central Sumatra/west Java and northern Sumatra, and (iii) three species in Africa—*H. natalense* in eastern Cape Province, Natal and Transvaal, *H. wilmsii* in the same general regions and also eastern Zimbabwe and central Madagascar, and *H. peplidifolium* from eastern Zimbabwe north to Ethiopia and west to Angola, the Cameroon Highlands and Fernando Poo (Robson, 1958*b*, 1961, 1973*a*, 1974; Bamps, 1971 Killick & Robson, 1976). All three groups seem to be related directly to the New Guinea one, *H. natalense* being particularly similar to the widespread New Guinean *H. papuanum*.

(*i*) *Old-World transcontinental distributions. II. Sects 27–28* (Figs 67, 69)

Sect. 27. *Adenosepalum* comprises two groups (subsections ?), both of which have their most primitive species in Macaronesia. The species nearest to sect. 1. *Campylosporus* is *Hypericum glandulosum* (western Canary Is.; Madeira), to which is allied a group of tropical and southern African species which are completely glabrous (Robson, 1958*b*, 1980*a*). Like the whole section, which has a markedly dissected distribution, these African species occupy widely scattered areas: *H. kiboense* in east Africa, *H. conjungens* in the Lake Tanganyika/Lake Nyasa area, *H. abilianum* in Angola (Huila) and *H. aethiopicum* (two subspecies) in the Zimbabwe/Mozambique border area, Angola (Huila) and South Africa (Robson, 1980*a*).

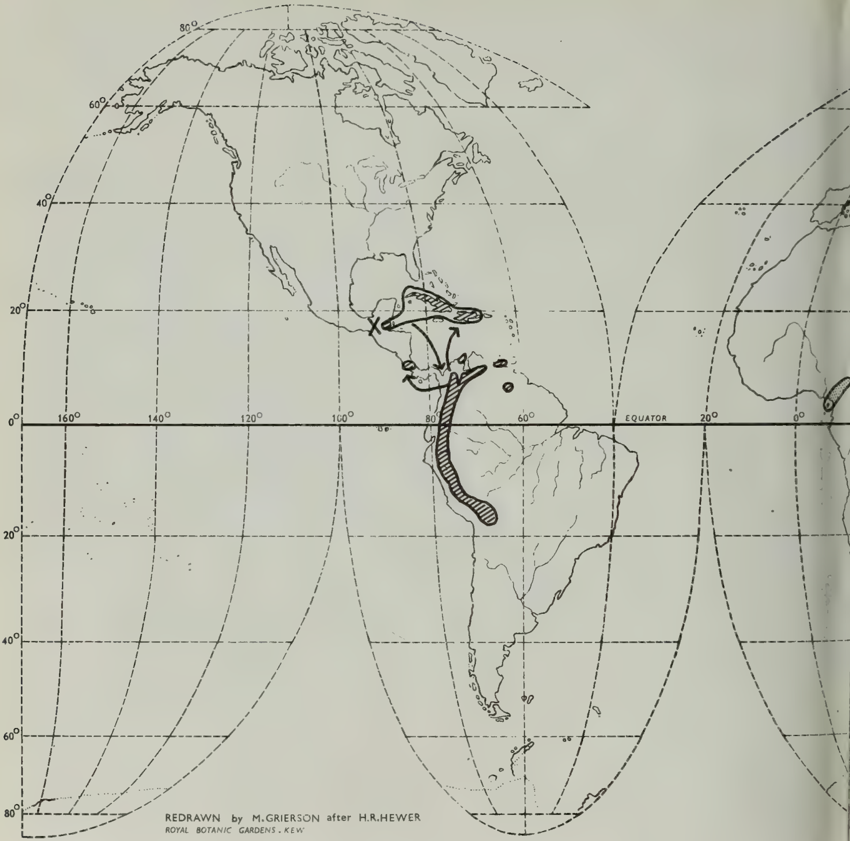
The other group stems from *H. reflexum* sens. lat. (western Canary Is.), a shrub with pubescent stems, and its relatives are probably primarily pubescent, i.e. there is evidence that the wholly glabrous species are secondarily so. They derive more immediately from *H. annulatum*, a variable (rarely glabrous) species with its most primitive form in Ethiopia/Eritrea ('*H. intermedium*') and apparently conspecific populations in east Africa ('*H. afromontanum*'), the Balkan Peninsula ('*H. degenii*') and Sardinia (*H. annulatum* sens. str.). *H. annulatum* is very closely related to *H. montanum* (central and west Europe, north Africa, the Crimea and western Transcaucasia) and some eastern Mediterranean species. Other Mediterranean, north African and Canary Island species show direct connections with the north-west African and western Mediterranean *H. pubescens* or its Somalian relative *H. somaliense*, the trans-Saharan gap being bridged to some extent by *H. psilophytum*, which occurs in the Hoggar Mountains (south Algeria).

The Asian species of sect. *Adenosepalum*, also, are related directly to *H. annulatum*, but they are wholly glabrous. The most primitive species, *H. elodeoides*, is distributed along the Himalayan range from Kashmir to western Assam, with disjunct populations in Khasia, Yunnan and Assam/Burma; and derivative species occur outside that area in China (Kweichow), northern Thailand, Tamil Nadu (Madras) and Sri Lanka (Robson, 1977*b*).

As I have explained earlier (Robson, 1972*a* : 378), *H. elodes* (sect. 28. *Elodes*) is morphologically very close to sect. 27. *Adenosepalum*, if the floral specialisations are ignored. Its nearest relative in sect. *Adenosepalum* is clearly *H. coadunatum*, which occurs in the Canary Islands (Gran Canaria) and also in Morocco and Algeria. The Gran Canaria plants (*H. coadunatum* sens. str.) are the most similar to *H. elodes*, which has an 'Atlantic' distribution in western Europe and the Azores (Fig. 69). The north African *H. coadunatum* (= *H. naudinianum* Cosson) on the other hand, is scarcely distinct from *H. caprifolium* of south-eastern Spain.

(*j*) *Sect. 29.* Brathys (Fig. 70)

The most primitive species of sect. 29. *Brathys*, *Hypericum styphelioides*, occurs in southern Belize and Cuba, the form in Belize being less specialised. The most closely related derivative species (*H. phellos*, *H. magniflorum* and one hitherto undescribed) are all found in the Colombia-Venezuela border region, whence the section has spread along the Andes in both directions, east to Northern Venezuela (*H. caracasanum*) and Mt Roraima (*H. roraimense*) and south-west to Peru and Bolivia (*H. andinum*). Three species otherwise almost confined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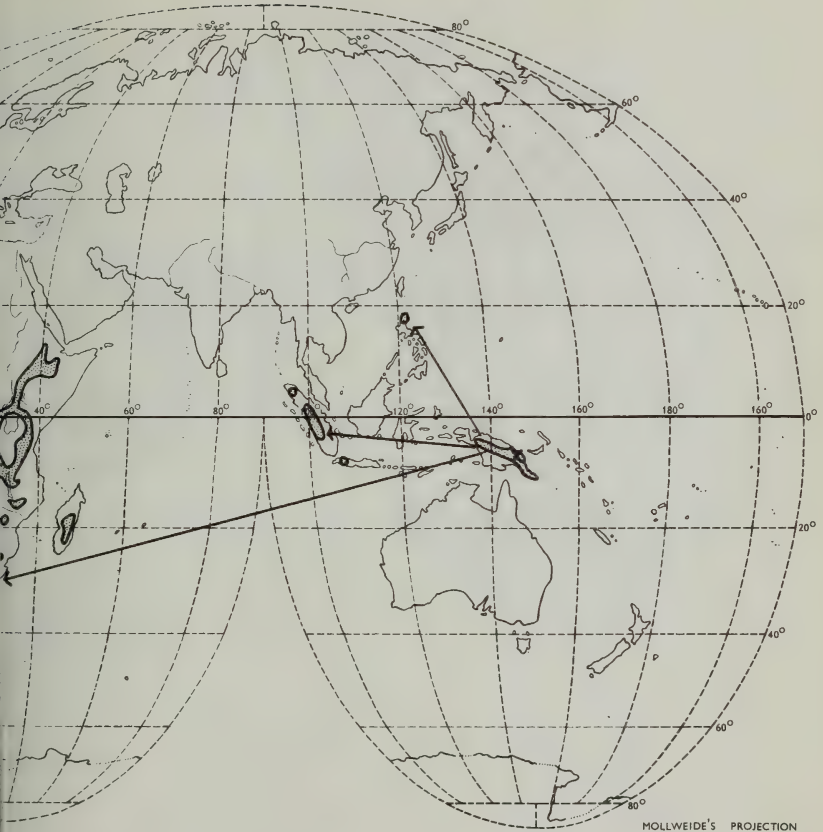
REDRAWN by M.GRIERSON after H.R.HEWER
ROYAL BOTANIC GARDENS. KEW

C.B.H. 4623 - Wt. 34154 - Dd. 10 - - 10/64

Fig. 70 Distribution of sects 2. *Psorophytum* ••••, 26. *Humifusoideum* ⁘ and 29. *Brathys* ▨. x = areas of most primitive species in sects 26 and 29.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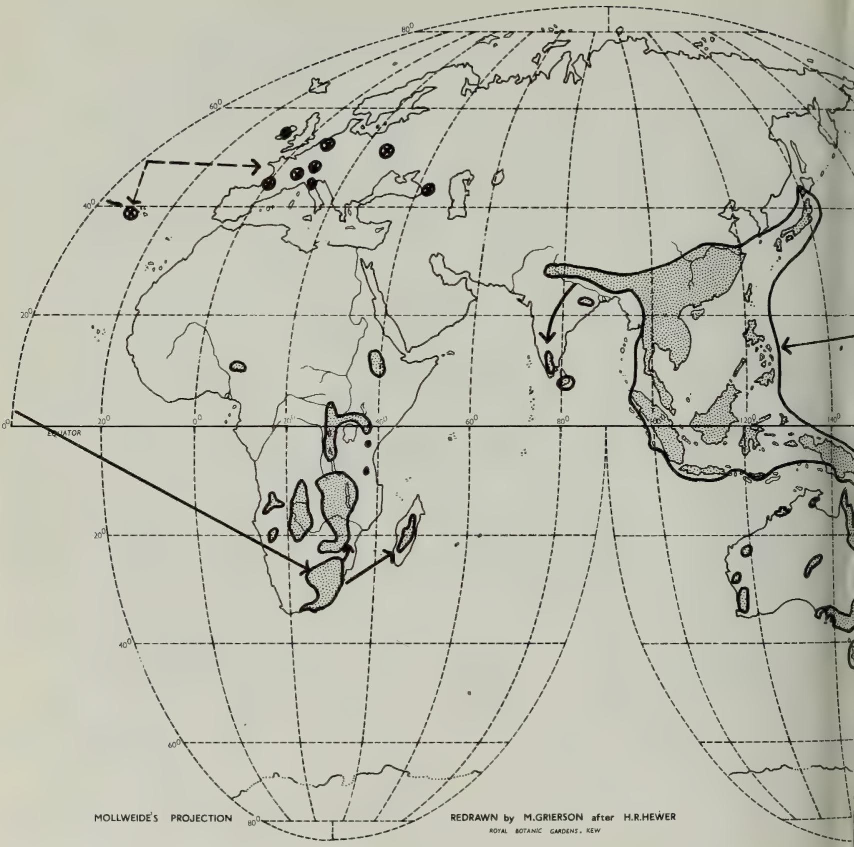
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REDRAWN by M.GRIERSON after H.R.HEWER
ROYAL BOTANIC GARDENS, KEW

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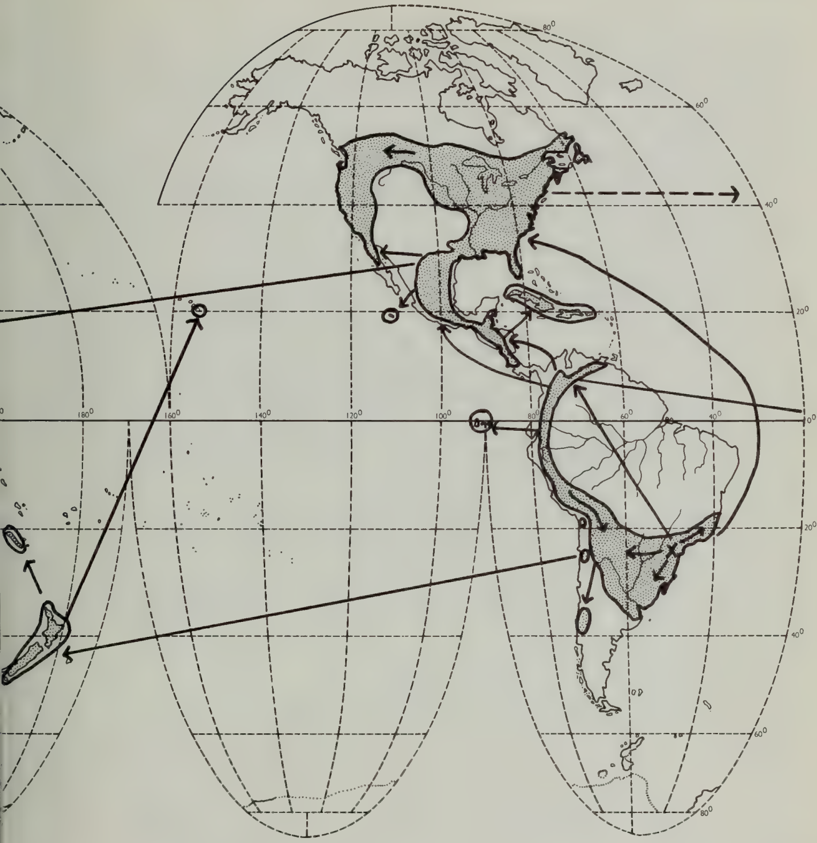
Fig. 71 Distribution of sect. 30. *Spachium*. x = area of most primitive species; ⊗ = apparently recent introductions.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to Colombia and adjacent Venezuela, or their close relatives, occur in the mountains of Costa Rica; and three other species, also with Colombian affinities, are endemic to Hispaniola.

(*k*) *Sect. 30.* Spachium (Figs 71, 72)

The widespread, intercontinental distribution of sect. 30. *Spachium* does not appear to make sense until morphological trends are considered; and, even then, no one theory seems able to account for it.

The most primitive species, *Hypericum rigidum*, occurs in southern Brazil and has its most primitive form in Paraná. It is clearly derived from the African *H. revolutum* subsp. *keniense* or from near it, and in turn it has given rise to a closely related group of species (*H. brasiliense*, *H. connatum*, *H. myrianthum*, etc.) in the region to the south of Amazonia, from the coastal range of Brazil to the Andean foothills of Bolivia. A group of North American species, *H. denticulatum* and its allies, in the south-eastern United States, is related directly to Brazilian members of this affinity.

Another derivative species of *H. rigidum*, *H. chamaemyrtus*, from the Andes of north-eastern Colombia, provides the key to the sectional relationships, as several trends appear to diverge from it. Of these derivative groups, only one species pair, *H. piriai* and *H. hilaireanum*, occurs in the above-mentioned southern area (in south Brazil and Uruguay). Although somewhat isolated morphologically as well, it is related to *H. gnidioides* and its allies, which extend in area from the Honduras Republic, where the primitive forms are found, south to Panama and north to Mexico and the Revillagigedo Islands. *H. gnidioides*, in turn, has derivative groups in the Greater Antilles (*H. dichotomum*, *H. fuertesii*, *H. diosmoides*) and the eastern United States (*H. drummondii*, *H. gentianoides*).

H. silenoides, a very variable species of the Andes from Venezuela to northern Argentina and the Galapagos Islands, is also directly related to *H. chamaemyrtus* through its most primitive forms, in southern Ecuador and northern Peru. It has given rise to *H. caespitosum* (*H. brevistylum* Choisy) of central Chile, which, according to Rodríguez-Jiménez (1973), is adventive in its north Chilean locality (Arica). The other Chilean coastal representative (*H. paposum* I. M. Johnston), however, cannot be differentiated from the protean *H. silenoides*. It is also very close indeed to the primitive forms of the E. Asian/Australasian *H. gramineum*, which are found in New Zealand, Tasmania and south-eastern Australia. This species shows three fairly distinct morphological and geographical trends (Robson, 1973*a* : fig. 3):

(1) New Zealand, New Caledonia, New Guinea, Taiwan.
(2) New Zealand, eastern Australia, eastern Himalayas.
(3) New Zealand, eastern Australia, western Australia, Vietnam.

The last group derived from *H. chamaemyrtus* comprises two subgroups, one mainly American and one African. *H. pauciflorum* of central and northern Mexico is the basic species of the first subgroup, and the areas of it and its immediate derivatives (*H. moranense* = *H. pratense* Cham. & Schlecht. sens. lat.) extend north to Texas and south to Panama. The remaining species are derived from *H. majus* of the northern United States and Canada, viz. *H. anagalloides* (western N. America), *H. canadense* (eastern N. America) and *H. gymnanthum* (south-eastern United States with a disjunct Guatemalan population). From the last-named there appear to have arisen two widely distributed species, *H. japonicum* and *H. mutilum.* The former has its primitive forms in the Philippines, Taiwan and adjacent China and extends north to Japan (southern Hokkaido), west to the Punjab and Sri Lanka and south to New Guinea, extreme south-eastern Australia and New Zealand (Robson, 1973*a*, fig. 5). The New Zealand form also occurs in Hawaii. The latter species (*H. mutilum*) is polymorphic and, although centred in the eastern United States and Canada, has disjunct populations in various parts of Central and South America and in the Azores, north-western France, northern Italy, Poland, Transcaucasia and Hawaii. In turn, it appears to have given

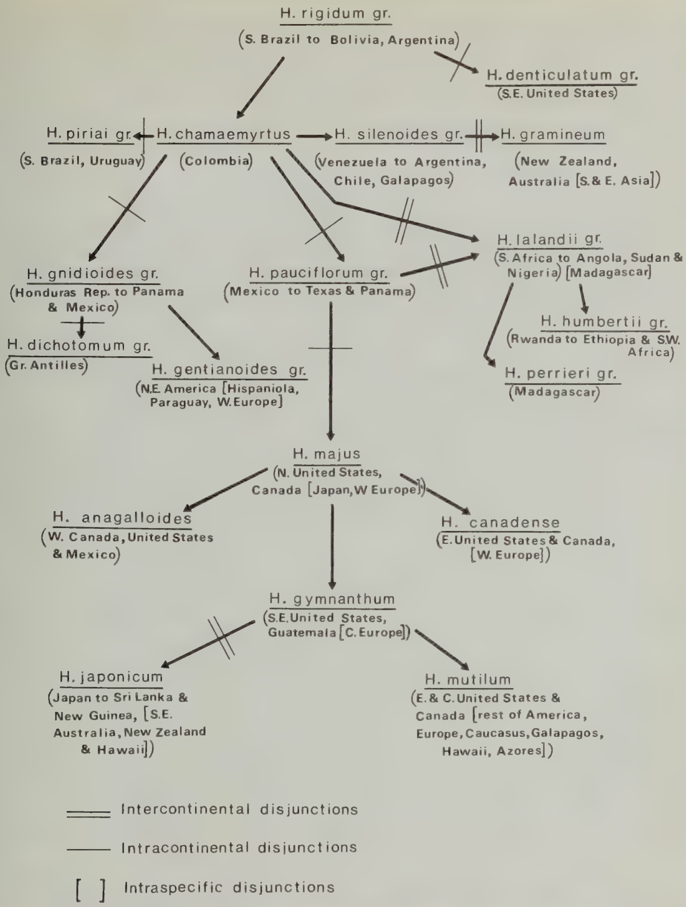
H. rigidum gr.
(S. Brazil to Bolivia, Argentina)
H. denticulatum gr.
(S.E. United States)
H. piriai gr.
(S. Brazil, Uruguay)
H. chamaemyrtus
(Colombia)
H. silenoides gr.
(Venezuela to Argentina, Chile, Galapagos)
H. gramineum
(New Zealand, Australia [S.& E. Asia])
H. lalandii gr.
(S. Africa to Angola, Sudan & Nigeria) [Madagascar]
H. gnidioides gr.
(Honduras Rep. to Panama & Mexico)
H. pauciflorum gr.
(Mexico to Texas & Panama)
H. humbertii gr.
(Rwanda to Ethiopia & S.W. Africa)
H. dichotomum gr.
(Gr. Antilles)
H. gentianoides gr.
(N.E. America [Hispaniola, Paraguay, W. Europe]
H. perrieri gr.
(Madagascar)
H. majus
(N. United States, Canada [Japan, W Europe])
H. anagalloides
(W. Canada, United States & Mexico)
H. canadense
(E. United States & Canada, [W. Europe])
H. gymnanthum
(S.E. United States, Guatemala [C. Europe])
H. japonicum
(Japan to Sri Lanka & New Guinea, [S.E. Australia, New Zealand & Hawaii])
H. mutilum
(E. & C. United States & Canada [rest of America, Europe, Caucasus, Galapagos, Hawaii, Azores])
Intercontinental disjunctions
Intracontinental disjunctions
[ ] Intraspecific disjunctions

Fig. 72 Evolutionary and geographical relationships in sect. 30. *Spachium.*

rise to *H. boreale* (north-eastern United States and Canada) (cf. Gillett, 1979), *H. arenarioides* (Cuba) and *H. pleiostylum* Rodr.-Jim. (eastern Brazil).

All the species of this subgroup except *H. anagalloides* and the *H. mutilum* derivatives have also been found in isolated localities in western or central Europe, as has *H. gentianoides* (cf. Heine, 1962; Robson, 1968*b*).

The second subgroup related to *H. chamaemyrtus* is African. *H. lalandii*, which is distributed from Cape Province to the southern Sudan and northern Nigeria (Bauchi) and also occurs in Madagascar, has its most primitive forms in Natal and the Transvaal. These are very similar to primitive Mexican forms of *H. pauciflorum* and a related species in the Colombian Andes, so much so that these three taxa are difficult to distinguish from each other. Within Africa and Madagascar, however, the variation in *H. lalandii* is great; and it appears to have given rise to distinct species groups in Madagascar (*H. perrieri* group) and east Africa (*H. humbertii* group). The latter extends north to Ethiopia and south-west to the Caprivi Strip.

Interpretation of *Hypericum* distribution

(*a*) *Introduction*

From the geographical relationships depicted in Figs 60 and 61 it is clear that *Hypericum* must have spread from Africa to the adjacent continents or, rather, to the continents that were adjacent in Gondwanaland before that supercontinent began to break up. *Hypericum* and *Santomasia* can thus be interpreted as Hennigian sister-groups, one in the east and the other in the west of west Gondwanaland. The present relict distribution of *Santomasia* on either side of the Mexico-Guatemala border (in an area that was not part of Gondwanaland) could be regarded as secondary, i.e. to have been attained after North America made contact with South America. Alternatively, but less likely, it could have been attained via north Africa and eastern North America.

At the outset of this analysis of *Hypericum* distribution, it is necessary to clarify two points, relating respectively to dispersal and time of origin:

(1) The natural distributions of all sections of *Hypericum* can be harmonised with current theories of plate tectonics, with the apparent exception of sect. 30. *Spachium*. In general, therefore, it seems unnecessary to involve long-distance dispersal in the interpretations. Even though the seeds of *Hypericum* are small, there is no direct evidence of intercontinental transport by birds (cf. p. 124), wind or air-currents; the evidence of such transport in sect. *Spachium*, although apparently strong, is circumstantial.

(2) There is no unequivocal fossil evidence for the existence of angiosperms before the Early Cretaceous (Hickey & Doyle, 1977; Hughes, 1977); and the earliest fossils that do exist are of monocolpate pollen grains, whereas those of the *Dilleniidae* (including *Hypericum*) are basically tricolpate. Some workers therefore deny that the angiosperms could have originated much earlier than the Cretaceous without detection; others, considering their undoubted diversification into modern families by the Middle Cretaceous at least, believe that they must have had a long pre-Cretaceous existence (cf. Lakhanpal, 1976). To some believers of the former theory (e.g. Smith, 1973; Thorne, 1975), the break-up of Gondwanaland started too early to be relevant to any angiosperm distribution. To others (including myself), the distribution patterns that are found at present are so consistent with the plate tectonics theory that they must have been achieved with the help of continental drift. Such workers are thus forced to adopt the hypothesis that the early history of the angiosperms extends back to well before the Cretaceous, but that angiosperm fossils from that period have not been found or, more likely, have not been recognised.

As the distribution of *Hypericum* seems to be interpretable only in terms of the plate tectonics theory, therefore, we are forced to postulate that the genus originated before direct land connections between Africa and the other parts of Gondwanaland were broken or, at least, before the areas of water between these continents became uncrossable by seeds or other diaspores.

(*b*) *Sect. 1.* Campylosporus *and the Macaronesian-Mediterranean area*

Whatever theory of plate tectonics that one adopts to reconstruct the distribution of continents before the break-up of Gondwanaland, the regions indicated in Figures 60 and 61 are brought together round Africa (Fig. 73a, b).

The least controversial distributional connections are those between Socotra and north-eastern tropical Africa, on the one hand, and Macaronesia and the Mediterranean area on the other (sects 2, 21–25, 27) (Figs 60, 61: tracks v, vii *a*). The disjunctions along these tracks are clearly due to the alpine orogeny and the formation of the Saharan desert belt. The northward migration of Africa resulted in the establishment of dry-land connections between Africa and Europe during the Cretaceous (between 148 and 80 m.y. BP) (Raven & Axelrod, 1974; Raven, 1979). Whether north Africa and Macaronesia were part of Gondwanaland (Smith, Briden & Drewry, 1973) (Fig. 73a) or Atlantica (Melville, 1973 & ined.) (Fig. 73b) does not affect the issue. Sect. 23. *Triadenioides* will have had a dry-land link between Socotra and the Levant, and will have been able to reach Anatolia by the Eocene (Raven, 1979); and the species of sects 24. *Heterophylla* and 25. *Adenotrias* are scattered round Morocco and the Mediterranean, mostly near the coast, as a result, presumably, of migration across the Saharan region by their ancestors. Of the Macaronesian sections, sect. 21. *Webbia* is a typical relict group with derivative relations in the Mediterranean (sect. 22. *Arthrophyllum*). Sect. 27. *Adenosepalum*, in contrast, has primary derivative links with tropical Africa and only secondary ones across the Saharo-Sindian desert to (i) the Mediterranean and western Europe (including sect. 28. *Elodes*) and (ii) the Himalayas and south-east Asia.

(*c*) *Sect. 20.* Myriandra

The disjunction between north-eastern Africa and the south-eastern United States (Figs 60, 61: track vii *b*) indicates that the ancestors of sect. *Myriandra* must have crossed from Africa to North America before the Atlantic Ocean was formed, i.e. in the Jurassic (180 m.y. B.P.), or soon after its initiation. This long period of separation is consistent with the considerable morphological discontinuity between sects *Campylosporus* and *Myriandra*. Subsequent migrations within sect. *Myriandra* have no doubt been mostly over land, even to Cuba, which was probably reached via Mexico and Belize as well as from Florida (cf. Rosen, 1976, for links between Mexico and the Greater Antilles).

(*d*) *Sect. 3.* Ascyreia *and its derivatives*

The close resemblance between *Hypericum revolutum* subsp. *keniense* (sect. *Campylosporus*) and *H. mysurense* of south India and Sri Lanka (sect. *Ascyreia*) supports the theory that the latter's ancestors reached the Indian plate before it broke away from Africa in the Mid-Cretaceous (*c*. 90–100 m.y. B.P.) (Raven, 1979). After the Indian plate abutted on Asia (45 m.y. B.P.), the species of sect. *Ascyreia* could have migrated across land to Europe, China and Malesia. The gap in distribution between the Himalayas and Anatolia (*H. calycinum*), as well as those between the Himalayas and the Caucasus (*H. xylosteifolum*—sect. 6. *Inodorum*) and Macaronesia (*H. grandifolium*—sect. 5. *Androsaemum*), indicates that an early westward trend was established by species of mesophytic habitats. These species are related respectively to *H. oblongifolium* (*H. calycinum*) and *H. griffithii* (*H. grandifolium*, *H. xylosteifolium*). Another, possibly later, westward trend comprising species related to *H. cordifolium* and *H. podocarpoides* apparently gave rise to more xerophytic species, the progenitors of the *Olympia* group (sects 10–16) and the *Hirtella* group (sects 17–19). In both these groups there is a gap between the Himalayan relatives and the Anatolian centre of variation—west Anatolia for the former, east Anatolia for the latter.

The ancestors of sect. 4. *Takasagoya* probably reached Taiwan before it was separated from the Asian mainland, but whether the further migration to Luzon was over land or not is unclear.

The other eastward development from sect. *Ascyreia* is that of sect. 7. *Roscyna* and its derivatives, sects 8–9a. The morphological gap between sects 3 and 7 is small, as is the geographical one (in China) between the areas of *H. monogynum* and *H. elatoides*. On the other hand, the whole of the central Asian plateau and desert area lies between the central and west Chinese *H. elatoides* group (*H. elatoides*, *H. pedunculatum*, *H. przewalskii*) and the west Transcaucasian *H. bupleuroides* (sect. 8. *Bupleuroides*), which suggests that the westward migration of the ancestor of *H. bupleuroides* occurred before the elevation of the Tibetan plateau.

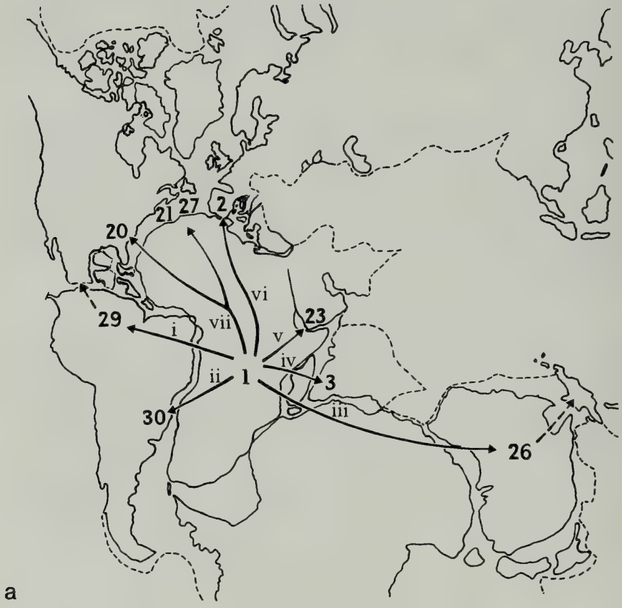
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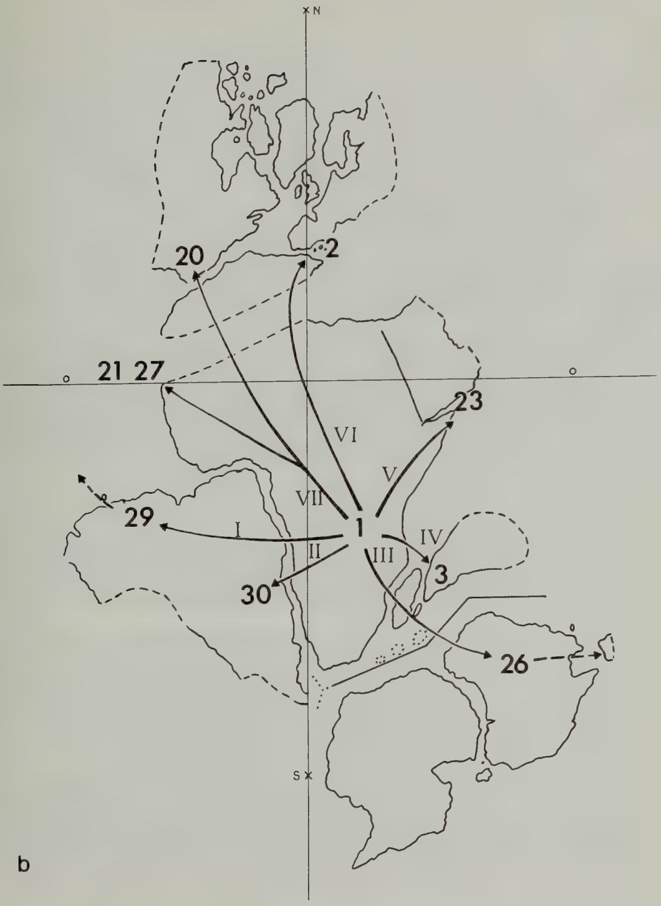
Fig. 73 Two reconstructions of Gondwanaland and the north Atlantic area in the Triassic; (a) according to Smith, Briden & Drewry (1973); (b) according to Melville (ined.). In both reconstructions, solid lines indicate present shores, interrupted lines boundaries now on land, and dotted lines continental edges or fragments now submerged.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b

Within one species of sect. *Roscyna*, *H. ascyron*, there is a wide disjunction between the Asian and eastern North American parts of its distribution. No evidence has been found to suggest that this species ever occurred in Europe,* and so the distributional links are likely to have been trans-Pacific. This hypothesis is made more likely when the trans-Pacific link between Asiatic forms of *H. ascyron* and the derivative Californian *H. concinnum* (sect. 9a. *Concinna*) are taken into consideration. The Bering bridge would seem to have been the route by which these species reached North America, if one accepts current orthodox views of plate tectonics in the Pacific area (cf. Raven & Axelrod, 1974). Even if Melville (1981) is correct and a Pacific continent did exist, it could not have provided a land-bridge directly from China to America for these species. By the time that the ocean gap between Asia and the western part of 'Pacifica' had narrowed sufficiently to allow the progenitors of sect. *Roscyna* to migrate there, the western (Chinese) and eastern (western North American) parts of that hypothetical continent would have been separated by a wide stretch of ocean.

From similar considerations, it seems likely that the trans-Pacific link in sect. 9. *Hypericum* also indicates a Bering bridge migration in this section. The present-day nearest relatives are respectively in central China (*H. pedunculatum*, sect. *Roscyna*) and Mexico (see p. 192); but despite the more southerly distribution of the primitive species of American sect. *Hypericum*, there is no evidence of a southern origin of this group, i.e. of a northward divergence from 'Pacifica'. Other genera with east Asian/Mexican disjunct areas are discussed by Styer & Stern (1980), who suggest that they may all have had Tertiary pan-boreal distributions.

To the westward, the *H. maculatum—H. tetrapterum* group reached western Europe and north Africa, apparently via a northern route and at a time when the Azores (*H. undulatum*) and the Faeröes (*H. maculatum*) were still reachable by land. *H. perforatum* penetrated west as far as the Canaries, south to Jebel Marra (Sudan Rep.) and east to China, apparently by natural means;† but its occurrence in Japan may not be due to natural spread, and its presence in North and South America, South Africa and Australasia is certainly the result of introduction.

(*e*) *Sects 1.* Campylosporus *and 26.* Humifusoideum

The first part of track iii (Figs 60, 61) has been considered in an earlier paper (Robson, 1979), where I discussed the close relationship between the *Hypericum revolutum* (African mainland) and *H. lanceolatum* (Mascarene Is.) groups, and the apparent parallel evolution that they have undergone.

It was there concluded that they diverged from an ancestral species that probably occupied a single area in the east Africa-Madagascar-Mascarene region in the Cretaceous era, before these land blocks were separated by rift and drift. Although I accepted an original northern position for Madagascar in this paper (cf. Wild, 1975) (Fig. 73a), the evidence would fit in equally well (or better) with a southern position beside Mozambique (Fig. 73b). In addition, a southern position would make the distribution of sect. 26. *Humifusoideum* easier to interpret (cf. Melville, 1975).

Sect. *Humifusoideum* has its primitive group of species (five in number—Robson, 1973*a*, 1974) in the mountains of New Guinea. The most primitive of these, *H. sewense*, is most similar to *H. lanceolatum* (Réunion, Comoro Is.) and *H. madagascariense* (Madagascar). We can thus postulate a migration from the Madagascar-Mascarene region to Australia, with subsequent migration to New Guinea (Fig. 73b). Van Steenis (1979) explains how, in the Mid-Tertiary period, the Australian plate is thought to have made contact with east Malesia.

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*Reid & Reid (1915) record a seed from Pliocene deposits near the Dutch-German frontier as '*Hypericum* cf. *ascyron*'. A study of the specimen leads me to doubt if it belongs to *Hypericum* at all. It certainly cannot be regarded as good evidence for the occurrence of *H. ascyron* in Europe.

†Wickens (1976), however, suggests that it may have been introduced to Jebel Marra by man.

At the same time the previously archipelagic New Guinea region gradually emerged above the sea to form a large continuous land mass. The luxuriance of the subsequent influx of the Malesian element of the flora would have overwhelmed the Australian-Gondwanean element, suffocating it or allowing it to survive mainly in the recently formed mountains. The species of sect. *Humifusoideum* would then probably have died out in Australia as a result of the ensuing period of drought (Kemp, 1978).

The diversification of sect. *Humifusoideum*, however, must have taken place before direct or indirect contact between Africa and Australia was lost in the Cretaceous period (Raven & Axelrod, 1974). The most primitive African species, *H. natalense*, is very similar to the mostly widely dispersed New Guinea species, *H. papuanum*; so it seems that representatives of sect. *Humifusoideum* must have reached the African mainland after speciation had occurred in Australia. *H. natalense* is confined to extreme south-eastern Africa, but the derivative *H. wilmsii* has a disjunct distribution in South Africa, the eastern border of Zimbabwe and Madagascar. Therefore, unless Madagascar was reached by long-distance dispersal (for which there is no evidence), this is another reason for putting the original spread of the African species back to the era before contact between Africa, Madagascar and Australia was finally broken, about 140 m.y. B.P. (Melville, 1975). India may or may not have been part of the relevant area of contact (Fig. 73b). At any rate, this section does not occur in India or Sri Lanka today; and the occurrence in that region of sect. 3. *Ascyreia*, on track iv, would suggest that sect. *Humifusoideum* (on track iii) took a more southerly course. These considerations all favour a reconstruction of Gondwanaland (such as that in Fig. 73b) where Madagascar has a southern position and is close to Australia, rather than one (such as in Fig. 73a) where it has a northern position and Australia is separated from Africa by Antarctica.

The above reconstruction of events does not, however, account for the occurrence of *H. pulogense* in the mountains of Luzon (Philippines) and of *H. beccarii* in scattered regions of Sumatra and west Java. These species are advanced relative to the New Guinea ones and well separated from them morphologically as well as geographically. It is quite possible, then, that they have reached their present areas of distribution gradually over land, possibly when the Sunda shelf was largely dry land during the Glacial Epoch (van Steenis, 1979). *H. pulogense* is on van Steenis's New Guinea track (New Guinea to Celebes and the Philippines), one of the dispersal routes that he distinguished when discussing the origin of the Malaysian mountain flora (van Steenis, 1934). The occurrence of *H. beccarii*, on Sumatra and Java, on the other hand, is less easily explained. Perhaps it reached these islands via Sulawesi.

(f) Sect. 29. Brathys

Similar arguments to those that have been adduced to explain the occurrence of sect. 20. *Myriandra* in Belize and Cuba as well as in eastern North America can explain the presence of the primitive species of sect. 29. *Brathys* (*Hypericum styphelioides*) in Belize and Cuba (Figs 60, 61: track i). The more southerly distribution of the primitive members of the section can be correlated with the more southerly distribution in Africa of its nearest relative (*H. revolutum* subsp. *keniense*); but too much emphasis should not be placed on this argument. It is more important to emphasise the 'vicariance model of Caribbean biogeography' described by Rosen (1976), whereby the original link between North and South America, in the late Mesozoic, was via the proto-Antilles, from Yucatan via Cuba, Hispaniola, Puerto Rica and the Lesser Antilles, which at that time are thought to have formed a connecting archipelago. When North and South America began to move westward from Africa, the proto-Antilles archipelago moved less quickly and was deformed to an arc. Subsequently, in the Middle to Late Tertiary, another volcanic archipelago was formed between Mexico and Colombia, and this consolidated to produce the present Central American isthmus.

This reconstruction implies that the ancestors of sect. *Brathys* reached America from Africa in one of two ways. (i) They may have arrived first in northern South America, speciated there and migrated early northward along the proto-Antilles in two or three waves, the first of which (*H. styphelioides*) reached Belize and Cuba whereas the second (*H. millefolium*) and third (?) (*H. pycnophyllum*) only reached Hispaniola. (ii) Alternatively, they may have arrived first in the extreme south of the North American plate, in Belize and Cuba, migrated southward along the proto-Antilles, and subsequently retraced their tracks as far as Hispaniola. Of these two possibilities the first involves the more direct routes and is therefore the preferred hypothesis.

Whichever way the original migrations occurred, there has clearly been much subsequent movement to-and-fro along the Andean range; and the Costa Rican mountains have been reached from South America by three species that are not closely related to one another (*H. stenopetalum*, *H. caracasanum*, *H. strictum* sens. lat.). In addition, the presence of an endemic species on Mt Roraima (*H. roraimense*) may well date from an earlier period in the evolution of sect. *Brathys*, i.e. before the Andean range was formed, as this mountain is part of the ancient Guyana Highland (Maguire, 1970).

(*g*) *Sect. 30.* Spachium

It has been possible to explain the distribution of previous sections without recourse to a hypothesis of long-distance dispersal. This is not to deny, of course, that such dispersal has occurred in them, but only to point out that it need not have done so. In sect. 30. *Spachium*, on the other hand, we are faced with a section of which the current distribution is apparently partly inexplicable except in terms of long-distance dispersal. This exceptional behaviour, moreover, becomes more plausible if one considers the habit and habitats of the relevant species. They are all annual or shortly perennial herbs of wet places (ditches, river banks, lake margins, rice fields), with seeds that are relatively small for *Hypericum*. These considerations make them eminently suitable for dispersal in mud attached to the feet of birds, although there is no direct evidence for this (see p. 124).

The differences between *H. revolutum* subsp. *keniense* and *H. rigidum*, the most primitive species in sect. *Spachium*, are both considerable and consistent with the hypothesis that the ancestors of these taxa diverged before South America broke away from Africa in the Cretaceous. *H. rigidum*, in southern Brazil, occupies one of the most ancient continental areas in South America. This hypothesis is also supported by the existence of a closely related and taxonomically difficult group immediately related to (derived from ?) *H. rigidum* in the area to the south of Amazonia, stretching from the Brazilian coastal mountains to the foothills of the Andes in Bolivia (Fig. 71). This group of species (the *H. brasiliense—H. connatum* group) must have evolved over a long period in order to produce 22 species that are morphologically so varied. Yet, the fact that the gaps in this variation are mostly small suggests that confinement to the region between the hot wet Amazon and the cool dry pampas has resulted in repeated partial isolations and hybridisation, again over a long period.

The disjunction between the *H. denticulatum* group of south-eastern U.S.A. (*H. denticulatum* sens. lat., *H. setosum* and *H. cumulicola*) and its nearest relatives, in southern Brazil (*H. cordiforme* and *H. ternatum*) is difficult to interpret other than in terms of ancient long-distance dispersal. The morphological gap between *H. denticulatum* and the Brazilian species is not great.

The rest of this large section is apparently derived from near *H. chamaemyrtus*, a relict species of the Colombian Andes that occurs in distinct forms in two relatively widely separated localities (provinces Santander and Cundinamarca). *H. chamaemyrtus* appears to be directly but rather distantly related to *H. rigidum*; but the areas of these species are separated by the whole width of the Amazonian rainforest, a region that has been drier than it is at present (Prance, 1978). It seems possible, then, that the ancestors of *H. chamaemyrtus* migrated (i) directly over this area or (ii) via the (new) Andes, or that (iii) the ancestors of *H. rigidum*/*H. chamaemyrtus* occupied some intermediate area. The Andean route would seem to be the most likely of these possibilities (cf. Simpson, 1975).

Not only is *H. chamaemyrtus* taxonomically isolated, but it is the apparent origin of several separate evolutionary lines, all of which show more-or-less wide disjunctions (Figs 71, 72). In one line, in which the basic chromosome number (x) is 12, the gap between Colombia and the Honduras Republic (*H. gnidioides*) is consistent with a migration through the proto-Antilles to Central America, whence there is a secondary radiation involving further disjunctions. There are, and were, direct overland connections south to Panama and north to Mexico for *H. gnidioides* and some derivative species, and the *H. dichotomum* group (Greater Antilles) could have diverged from Central America back along the proto-Antilles; but how *H. eastwoodianum* reached the Revillagigedo Islands is not clear, as this species also occurs in western Mexico (Jalisco, Zacatecas). *H. drummondii** and *H. gentianioides*, of the eastern United States, may well have reached their present area over land from Mexico; but the remaining species in this line, *H. piriai* and *H. hilaireanum* of southern Brazil and Uruguay, have links across Amazonia again. These species are morphologically isolated in the section and appear to represent an early southward migration from the *H. chamaemyrtus*/*H. gnidioides* line.

H. pauciflorum is also closely related to *H. chamaemyrtus*. It and its immediate descendents have spread north and south along Central America, but from a more northern centre (Mexico), north to Texas and south to Panama.

There is then a disjunction northwards to the *H. majus* group, all of which have n = 8, and all except *H. anagalloides* (western United States and Canada) have apparently indulged in long-distance dispersal. Thus *H. majus* itself (northern United States and Canada) also occurs in France and Germany and has recently been found in Japan (Hokkaido) (*Hara, Kurosawa & Inteishi* 13.ix.1974, **TI**), *H. canadense* (north-eastern United States and Canada) also occurs in western Ireland and the Netherlands, and *H. gymnanthum* (south-eastern United States) also occurs in Guatemala and Poland. *H. gymnanthum*, in turn, has given rise to two widespread groups:

(i) *H. mutilum* (possibly including *H. boreale* (Gillett, 1979)) is native to the eastern and central United States and Canada; but it has been found in many other parts of the world, viz. Mexico, Honduras Republic, Cuba, Hispaniola, Colombia, Ecuador, Brazil, Paraguay, Uruguay, Argentina, Peru, Hawaii, the Azores, France, Italy, Poland and Transcaucasia. Some of these introductions have probably been recent (e.g. to Italy and Hawaii); others must be of considerable antiquity, because *H. pleiostylum* (eastern Brazil) and *H. arenarioides* (Cuba) are both apparently derivatives of *H. mutilum*.

(ii) *H. japonicum*, a widespread and variable ricefield weed of east Asia, has many wide disjunctions in its total area (see p. 206 and Robson, 1973*a*). Like the other species just mentioned, its distribution seems capable of interpretation only in terms of long-distance dispersal (by birds ?). The original dispersal from Texas (?) to south-east Asia, like the long-distance ones of *H. mutilum*, must have been of considerable antiquity for the species to have achieved its present wide distribution and varied morphology.

The very close morphological links between Mexican *H. pauciflorum* and a related species in the Colombian Andes, on the one hand, and primitive forms of *H. lalandii* in Natal and the Transvaal, on the other, may be the result of direct intercontinental migration. If, however, one considers (i) the apparently long prior evolution of sect. *Spachium* in South America, (ii) the northward African trends in the *H. lalandii* group and (iii) the apparent behaviour of some other herbaceous members of this section, then ancient long-distance dispersal from northern South America or Central America seems a much more probable explanation of the present disjunction. The presence of *H. lalandii* and the derivative *H. perrieri* group in Madagascar would then probably be best explained by long-distance dispersal from the African mainland. The other descendents of *H. lalandii* (*H. humbertii*, *H. scioanum* and *H. oligandrum*) are all confined to the African mainland.

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*Reid (1923) identified Pliocene fossil seeds from Pont-de-Gail, Cantal, France as belonging to *Hypericum* (*H. cantalense* E. M. Reid) and compared them, and other Pliocene seeds from the Dutch–German frontier at Reuver, with *H. drummondii*. The comparison does not seem very apt to me, and I doubt very much if the seeds do belong to *Hypericum*.

Finally, the distribution of the *H. silenoides* group is problematic. This species is clearly derived from the Colombian *H. chamaemyrtus* and has primitive forms in two areas, the Ecuador-Peru border (*H. silenioides* sensu stricto) and northern coastal Chile (*H. paposum* I. M. Johnston). From the former area there are gradual morphological trends along the Andes northward to Venezuela and southward to northern Argentina, as well as a fairly wide geographical disjunction between Bolivian forms of *H. silenoides* and *H. caespitosum* of central Chile. The nearest relatives of '*H. paposum*', on the other hand, are separated from it by the width of the Pacific Ocean. They are the most primitive forms of *H. gramineum*, which occur in New Zealand and south-eastern Australia. This distribution at first suggests an Antarctic distribution pattern; but, whether Magellania was part of South America when it split from Africa (e.g. Smith, Briden & Drewry, 1973) (Fig. 73a) or not (Melville, 1966) (Fig. 73b), it would not have been possible for the ancestors of *H. gramineum* to have reached there from northern South America at a time when the Antarctic migratory path was continuous. Thus, here again we seem to be faced with an ancient long-distance dispersal, this time between western South America and Australia/New Zealand. Whether or not this disjunction was the result of long-distance dispersal, however, there seems to be no doubt that the subsequent spread of *H. gramineum* (from (i) New Zealand to New Caledonia, New Guinea and Taiwan; (ii) Australia to Vietnam and the eastern Himalaya) was by this means (cf. Robson, 1973*a* : fig. 3).

11. Summary

1. *Hypericum steyermarkii* Standley is more primitive than other species of *Hypericum* in having 5 sterile structures representing the antisepalous whorl of stamen fascicles. In other characters (e.g. leaf venation) it is more advanced. It has therefore been removed to a separate genus, *Santomasia* **gen. nov.**
2. The Bonnetioideae sensu Maguire (1972), i.e. including the Kielmeyeroideae, should be included in the Guttiferae. Although this subfamily is more primitive in most characters than the Hypericoideae, it is not directly ancestral to the latter. Indeed, the three tribes of the Hypericoideae seem to show relationship to different parts of the Bonnetioideae.
3. Correlation of trends, rather than of characters, gives a more reliable indication of the course of evolution in a given taxon; and the mapping of correlated trends in modern taxa often suggests the direction in which the evolution has occurred.
4. A diagram showing the apparent relationships of the sections of *Hypericum* can be used to show the distribution of characters throughout the genus.
5. By back-projection of trends, it is possible to visualise the primitive *Hypericum* as being a tall shrub or small tree with 4-lined stem-internodes, entire sessile leaves having (i) a midrib and ± numerous veins that dichotomise at or near the base and then run parallel and (ii) pellucid, possibly only punctiform glands. The flowers were large, solitary and terminal, and bracteoles were not differentiated. The floral whorls were all 5-merous, the outer (antisepalous) whorl of stamen fascicles being absent. The sepals were completely free and, like the petals, entire with linear pellucid glands between the parallel veins. Dark glands were probably absent from all organs. The 5 antipetalous stamen-fascicles each had numerous stamens with filaments distinct from near the base. The pollen grains were prolate-spheroidal, with the endoaperture porate or almost so and the ornamentation possibly a tectum perforatum with tectal perforations grouped together. The ovary had 5 placentae, which formed a central column but were not markedly axile (i.e. not closely united), and was surmounted by 5 free but ± appressed styles. The seeds were numerous, probably narrowly unilaterally winged, and with a reticulate testa. *H. bequaertii* resembles this hypothetical ancestor closely.
6. From this hypothetical (but probably actual) species, evolutionary trends in various directions have resulted in: Shrubs or herbs with terete stem-internodes, leaves sometimes sub-petiolate, pinnate to reticulate-veined, rarely gland-fringed or scale-like, with dark punctiform glands; inflorescences of many small flowers, primarily cymose but occasionally partially racemose, with differentiated bracteoles; meiomerous floral whorls (the outer ones sometimes reduced to 4-mery, the gynoecium to 2-mery); sepals ± united, with punctiform pellucid or linear dark laminar glands and variously glandular or eglandular margin; petals remaining free, but otherwise varying like the sepals except

for the rare appearance of a ligule; stamen-fascicles united in various ways, sometimes with the disappearance of the common 'trunk', or rarely with the union of the filaments becoming more pronounced, and with a reduction in the number of stamens per fascicle; pollen becoming prolate with the endoaperture a lalongate colpus and the ornamentation reticulate with tectal perforations regularly spaced; the ovary with completely axile or completely parietal placentation and styles that are ± completely united or completely free and divergent; seeds without a wing or carina, the testa becoming ribbed and striate or papillose.

7. The primitive *Hypericum* flower is a brush blossom, open-pollinated by less-specialised insects (e.g. Syrphidae), which are attracted probably wholly visually by the 'target' appearance of the open flower (bee-yellow centre, bee-purple surroundings). In two separate sections, a change to specialised insect-pollination has been accompanied by the evolution of a pseudo-tubular flower and other modifications including, in sect. *Adenotrias*, dimorphic heterostyly. In both sections, members of the antisepalous stamen-fascicle have reappeared, acting like lodicules in opening the flower.
8. Seeds of *Hypericum* are small, but they appear to be dispersed largely by gravity. No long-distance dispersal has been demonstrated, although circumstantial evidence for this in sect. *Spachium* is strong.
9. Normally, *Hypericum* has a *Polygonum*-type embryo sac and the embryogeny is Solanad. Recorded abnormalities include polyembryony, pseudo-polyembryony (concrescence of ovules) and apospory. The germination is epigeal. The floral whorls initiate development in order centripetally, the sepals arising quincuncially, the petals simultaneously. The stamen-fascicles develop more quickly at first than do the petals, and the individual stamens arise in centrifugal succession on each fascicle primordium.
10. Variation in the vascular structure of the torus parallels that established from morphological studies, being interpretable in terms of a basic pattern of regularly pentamerous whorls, the three outer ones each with unilacunar traces. This variation enables one to discriminate between complete loss of an organ and 'loss' by union (i.e. loss of individuality). From a comparison of sections of the stele at toral level, it is possible to show that it has undergone both vertical and horizontal contractions.
11. Floral morphology and vasculature in *Hypericum* are most easily interpreted in terms of the Gonophyll Theory (Melville, 1962, 1963).
12. Variation in the essential oils of *Hypericum* is not of great taxonomic importance; but the presence and distribution of hypericin and pseudo-hypericin is characteristic and sometimes diagnostic of sections or groups of sections.
13. Counts of *Hypericum* chromosomes published since 1968 have confirmed the general picture described by Robson & Adams (1968), viz. a reduction of the basic number in different evolutionary lines from 12 to 6, with the occurrence of tetraploidy on most basic numbers. Higher polyploidy seems to be associated with reproductive abnormality. One secondary basic number (21) has been reported.
14. Natural hybridisation in *Hypericum* is uncommon. It has been shown to occur in sects 5. *Androsaemum* and 9. *Hypericum*, and its presence is suspected in sects 20. *Myriandra* and 30. *Spachium*.
15. Artificial hybrids have been confined mainly to sects 3. *Ascyreia* and 9. *Hypericum*. In the former section *H.* x 'Hidcote' is thought on circumstantial evidence to have resulted from crossing *H. calycinum* and *H. beanii* 'Gold Cup'.
16. In general: Crosses in *Hypericum* (i) often result in variegation, (ii) do not proceed beyond the seedling stage where different chromosome numbers are involved, and (iii) rarely yield seeds when 'wide'. When *H. perforatum* (4x) crosses with diploid species of sect. *Hypericum*, two forms of hybrid (3x, 5x) are produced.
17. *H. concinnum* Bentham is related to a different part of sect. 7. *Roscyna* from the other species in sect. 9. *Hypericum*. It has therefore been placed in a separate section, 9a. *Concinna* **sect. nov.**
18. Of the three tribes of the Hypericoideae: the Vismieae appears to be primitively South American and to have spread to Central America, Africa and Madagascar; the Cratoxyleae is primitively Malesian (or perhaps Madagascan) and has spread to eastern Asia and thence to (i) eastern North America and (ii) Mexico/Guatemala; and the Hypericeae is primitively African (*Hypericum*) and Central American (*Santomasia*).
19. Morphological and distributional trends in *Hypericum* indicate that the genus probably originated in tropical Africa and that it has spread initially to South America (sects 30. *Spachium* and ?29. *Brathys*), North America (sect. 20. *Myriandra*), north Africa, the Mediterranean and Socotra (sects 2. *Psorophytum*, 21. *Webbia*, 23. *Triadenioides*, 27. *Adenosepalum*), south India and Sri

Lanka (sect. 3. *Ascyreia*) and New Guinea (via Australia ?) (sect. 26. *Humifusoideum*). There is no evidence of long-distance dispersal at this stage. Indeed, all these migrations (of tree and shrub species) could have taken place over dry land if *Hypericum* originated and spread initially before the break-up of Gondwanaland; and the 'radiation' from Africa is best interpreted in terms of such a theory.

20. Subsequent evolution of herbaceous species in sect. *Spachium* has resulted in distributions strongly suggestive of long-distance dispersal, possibly by wading birds and waterfowl. Despite the evolution of many perennial and a few annual herbs in other sections, the evidence for long-distance dispersal elsewhere in the genus is almost absent, most distributions being interpretable in terms of over-land migration. Only in sect. *Hypericum* (mountains of Sumatra and Borneo) does such a migration seem unlikely.

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A revision of the lichen family Thelotremataceae in Sri Lanka

Mason E. Hale, Jr.

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A revision of the lichen family Thelotremataceae in Sri Lanka

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Synopsis

This paper presents a revision of the lichen family Thelotremataceae in Sri Lanka based on the historical collections of Thwaites and Almquist and those of recent workers. The morphology, chemistry, phytogeography and ecology of the family are discussed and keys and descriptions for 110 species presented. The following new species are described: *Thelotrema dissultum* Hale, *T. imperfectum* Hale, *T. leprocarpoides* Hale, *T. nureliyum* Hale, *T. pidurutalagalum* Hale, *T. pulvereodiscum* Hale, *T. scabiomarginatum* Hale, *T. subpatens* Hale, *T. waasii* Hale, *Myriotrema albocinctum* Hale, *M. decorticatum* Hale, *M. fissurinum* Hale, *M. fluorescens* Hale, *M. frondosum* Hale, *M. mastarion* Hale, *M. multicavum* Hale, *M. nuwarense* Hale, *M. polytretum* Hale, *M. protoalbum* Hale, *M. thwaitesii* Hale, *Ocellularia albomaculata* Hale, *O. ascidioidea* Hale, *O. croceopora* Hale, *O. exuta* Hale, *O. kanneliyensis* Hale, *O. keralensis* Patw. & C. Kulk. ex Hale, *O. lankaensis* Hale, *O. meiospermoides* Hale, *O. melanotremata* Hale, *O. neocavata* Hale, *O. neopertusariiformis* Hale, *O. pluripora* Hale, *O. rassagala* Hale, *O. rhicnopora* Hale, and *O. sticticans* Hale. One new combination, *Ocellularia polillensis* (Vainio) Hale, is made.

Introduction

One of the most remarkable yet little cited papers on tropical botany, 'The lichens of Ceylon', was published in 1870. In it the British lichenologist the Reverend W. A. Leighton

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listed nearly 200 species collected by G. K. Thwaites in Sri Lanka. A high percentage of these, some 44 species, were described as new. This pioneering effort in tropical lichenology was unfortunately not pursued further by Leighton, and he was soon eclipsed by the two giants of 19th century lichenology, W. Nylander and J. Müller (Argoviensis). Still, because Leighton antedates so much of their work, very few of his species have been relegated to synonymy, and they remain extremely important for tropical workers. The Thwaites' specimens on which Leighton based his accounts are now in the herbarium of the British Museum (Natural History), London; they comprise an important part of the tropical lichen collections.

Sri Lanka is an ideal place to conduct retrospective lichen research. With Thwaites' collections as a base, we can determine the extent to which the lichen flora may have changed in the past 100 years through deforestation for agriculture and commercial logging. I visited Sri Lanka twice, in 1976 and in 1978, with the express purpose of collecting and studying the Thelotremataceae, an important tropical crustose family which figures prominently in Leighton's flora. I was fortunate in having access to virgin dipterocarp forests being logged and succeeded in re-collecting most of the species reported by Leighton. At the same time I was able to add 76 species to the thelotreme flora to make a total of 110 species.

Historical background

Leighton's Ceylon lichen flora

The success of Leighton's work must begin with Thwaites' collections, for no herbarium of that day (and few even today) contained sufficient materials to prepare a revision of the lichens in any tropical country. G. H. K. Thwaites was appointed to the botanical post at Peradeniya, Sri Lanka, on 15 May 1849 by William Hooker. He served as director there from 1857 to 1880 and died in Kandy in 1882. During his tenure he not only maintained the well-known botanical garden and herbarium but conducted extensive field excursions to most parts of Ceylon, very early complaining in his letters to Berkeley about the land leeches which still plague collectors in the rain forest. Almquist called him an enthusiastic naturalist (Nordenskiöld, 1881). The accession books at the Royal Botanic Gardens in Kew are filled with entries of phanerogamic collections sent from 1850 to 1877. Many of these he had actually described himself while compiling a vascular flora of the island which eventually included 2832 species (Thwaites, 1864).

Thwaites had broad interests in botany and started collecting fungi soon after he arrived. He wrote to Berkeley as early as 10 September 1850 that he was going 'to send fungi and a few lichens this month'. They maintained active correspondence but lichens were only rarely mentioned again. Berkeley and Broome were eager to receive the fungi from this unknown tropical country and ultimately published on over 1000 species, describing hundreds as new (Berkeley & Broome, 1875) and encouraging Thwaites to continue collecting.

Since there was no lichenologist at Kew Gardens, Berkeley and Broome asked Thwaites to send the lichens directly to Leighton in Shrewsbury without passing through Kew. Thwaites wrote in April 1867 that he was sending some lichens and learned from Berkeley in December that Leighton was indeed beginning to study the material. We know from Leighton's letters to Nylander that three packages of lichens arrived between 25 November 1867 and 19 November 1868, and by 23 February 1868 Berkeley was able to tell Thwaites that the lichens were being actively studied. Thwaites had stipulated that one set should go to Kew, one be retained by Leighton, and a third be given to Nylander. In fact, Leighton sent only selected fragments to Nylander and the remainder was ultimately deposited in Kew [now tranferred to BM; see Brenan & Ross, 1970] as part of his bequest. By January 1869 the finished paper, 'The Lichens of Ceylon', was read before the Linnean Society of London. In

March 1872 Leighton told Berkeley that a few lichens remained to be described, but as far as I can determine he published nothing further on Sri Lanka.

One cannot help but wonder how Leighton found any time to work on lichens at all. He was very active as pastor in the church in Shrewsbury and once reminded Nylander that he had three children to raise. His first botanical endeavour was the preparation of a cryptogamic flora of the county of Shropshire, followed by a phanerogamic flora published in 1841. His early scholarly works were on the angiocarpous lichens (1851) and the British Graphidaceae (1854), studies which obviously prepared him for a better understanding of the numerous crustose families in Sri Lanka. His chief work was actually the impressive *The Lichen-flora of Great Britain, Ireland and the Channel Islands* (1871), one of the classics of British botany and the forerunner of Crombie's and later A. L. Smith's 'British Lichens'.

A rather intimate picture of Leighton's efforts to identify the Ceylon lichens, and the resources available to him, can be gleaned from his extensive correspondence with Nylander. From 1852 to 1874 he wrote about 120 letters to Nylander, often as frequently as one every two weeks. These are now part of the Nylander correspondence collection at the University of Helsinki library.

Leighton wrote in English since he confessed poor French and no knowledge of German, the reason he gave for later cancelling the subscription to *Flora, Jena* which Nylander had arranged for him. On 3 December 1853, Leighton sent Nylander a complete catalogue of his lichen library, which included most of the published works on lichens of that day. Nylander very generously helped fill out these holdings for the next 15 years. Most of the letters are in fact concerned with details of books and articles he asked Nylander to find and methods of payment (banks then as now were reluctant to handle small drafts), as well as lists of species unrepresented in his collection that he needed to see.

Leighton often enclosed small samples for comment or identification. Nylander helped identify the British Graphidaceae in this way, and many notes were exchanged on various species of *Lecidea* and other crustose genera, particularly between 1854 and 1865. Leighton also told Nylander of trips to Kew Gardens where he helped curate the Hooker Indian lichens. There must have been a small reference collection there since he looked for but could not find a specimen of *Heterodea* in 1866 and asked Nylander for one. He was as puzzled by this strange lichen as we are today.

Leighton thus not only had the benefit of many specimens verified or authenticated by Nylander and any specimens on file at Kew but also received a complete set of Wright's Cuban Lichens from Asa Gray in 1864, a set which is often cited in the 'Lichen flora of Ceylon'.

Nylander himself was unable to acquire this exsiccata and had to be satisfied with fragments from the set deposited in Paris. Leighton asked Nylander to add him to the list of subscribers for Lindig's Colombian lichens (24 May 1864), which Nylander had exhaustively studied and published on in 1863. Leighton did not obtain a set but probably examined one in Kew since he also cites it in the Ceylon flora. He asked 'Mr Krempelhuber' for specimens of his 'novelties' but once again he did not receive any. There are no Leighton specimens at all in Krempelhuber's herbarium (M), and Krempelhuber (1877) said that he saw none.

I was able to locate 23 specimens of the Thelotremataceae of Ceylon which are now preserved in the Nylander herbarium in Helsinki. All are small fragments, no more than 1–2 cm², mounted on the same faintly ruled or blue letter paper Leighton used in his correspondence. He clearly wrote the 'C. L.' (Ceylon lichens) number assigned by Thwaites along with his own determination. Nylander often added 'Thwaites'. Leighton told Nylander several times that he was only sending new species or otherwise interesting specimens so as not to burden him with too much work, and in fact samples of 10 species were not sent. In only one instance was a specimen sent without a name (C. L. 31, determined by Nylander as '*T. punctulatum* Nyl.'). Once Nylander annotated a specimen (C. L. 99, *Thelotrema sphinctrinellum*) as 'false determinato', a notation which Leighton ignored, since this name is in the published list of Ceylon lichens, and in a similar case, C. L. 19 (*Thelotrema albidiforme* Lgt. n. sp.) was redetermined correctly by Nylander as *T. porinoides* and later published as such (Nylander, 1900). Leighton did not change his mind here either, although he thanked Nylander several times for his corrections of the Thwaites' lichens.

Two contemporary British lichenologists were often mentioned in the correspondence: Babington, much admired by Leighton, and Mudd, the author of an earlier lichen flora of Great Britain. His relationship with Mudd was evidently hostile, since Mudd had reviled him for adopting Nylander's chemical tests ('the absurdity of using chemistry in taxonomy'). Leighton almost gleefully and with obvious sarcasm passed Mudd's comments on to Nylander and seemed to revel in his role as the proponent of chemical taxonomy in England. One should remember that it was Leighton who offered to translate Nylander's now historic article on the use of hypochlorite of lime and caustic potash (Nylander, 1866). He was, in fact, the first lichenologist to adopt colour tests after Nylander. This was even noted by Th. M. Fries (1871: 58) when he critically discussed the use of KOH by Nylander to separate closely related Cladonias, adding, with obvious concern, that Leighton had willingly followed Nylander by using CaCl in a similar way. He questioned emphatically but futilely: 'Num ad species distinguendas idoneae sunt notae chemicae?'. Later Nylander (1891:100) bitterly criticized Fries for these comments.

Leighton's independence and confidence in handling the Ceylon lichen identifications may well explain the drop in correspondence with Nylander after 1869. Nylander was more accustomed to receiving unidentified lichen specimens which he would be free to describe as new, being without question the leading lichenologist of the day. Leighton, however, did not even write to him about the publication of the Ceylon flora, even though he told Nylander on 12 April 1870 that he was working steadily on the 'Lichen-flora of Great Britain' and sent him a copy on 22 September 1871. In one of the last letters to Nylander (26 February 1874), Leighton replied 'to your not very courteous letter', that he was 'not quite so ignorant of "elementary botany" as not to know that zoospheres and spermatia are different organisms', obviously reacting to criticism from Nylander. As the final insult, Nylander transmitted his own paper in opposition to Schwendenerism to Crombie (1891), even though Leighton had earlier offered to translate it and get it inserted in *Grevillea* ('Your transfer of your paper to Mr Crombie only excites a smile').

Leighton finally gave up botany in 1879 because of failing eyesight and turned all of his collections over to Kew. He died 25 February 1888 (Phillips, 1889).

Little reference has been made to Leighton's Ceylon lichens since the 1870 publication. Krempelhuber (1877) was the first to cite them, without actually seeing the specimens, when he included five species described by Leighton in a monograph of *Ascidium* (*A. granulosum, A. pachystomum, A. pertusariiforme, A. punctulatum,* and *A. thelotremoides*). Nylander, as I mentioned above, used the names *Asteristion erumpens* and *Thelotrema albidiforme* (as a synonym of *T. porinoides*) in his list of the Almquists' collections. Although Vainio (1921) identified 30 species of thelotremes from the Philippines, 24 of them new, he referred to only one Leighton species, *T. pertusariiforme,* in a discussion of *T. curranii* Vain. He had seen the Ceylon specimen in Nylander's herbarium. As a matter of fact, I have identified only one Leighton species, *Ocellularia chonestoma,* from the Philippines.

The Thwaites' collections

Thwaites shipped his well-prepared and ample collections to Leighton glued on white sheets. For reasons we cannot even guess now, Leighton remounted virtually all of these on a heavy blue letter paper, transferring the label data in his own hand and discarding the original labels. In contrast, Berkeley and Broome kept the fungi on their original mounts. The number of unicate thelotreme specimens sent added up to at least 49, and there is reason to believe that more were sent but not accounted for. It is also unfortunate that Leighton ignored Thwaites' collection numbers in his final publication and simply numbered the species serially. One can be thankful that there is only rarely any confusion as to the collection used in the publication.

The localities for the Thwaites' lichens cannot be determined accurately except when he specifically refers to Peradeniya or Hakgala ('Habgalla'). The most frequent designations, 'Central Province' and 'South of island' are of no help. Notwithstanding, he collected many species, such as *Ocellularia chonestoma,* from the leech-infested low-elevation rain forests, along with obvious high-elevation species in the Horton Plains area, such as *O. fissa.*

After Thwaites received Leighton's published article, he transferred the names to sets of duplicate specimens preserved in Peradeniya along with a large series of duplicates for some of the numbers. Unfortunately, he further obscured the accuracy of the locality data by citing each species according to Leighton's published species numbers (1–196), omitting all other information on the original C. L. (Ceylon Lichens) numbers or localities, even though he prepared a list of the corresponding numbers for his own purposes. I discovered a notebook in the Peradeniya herbarium with a partial list of the institutions where sets were to be sent, as follows: a: [blank]; b: British Museum 1875 [BM specimens were subsequently stamped 'Ceylon, G. H. K. Thwaites, Rec'd. 1875']; c: [blank]; d: Geneva Prof. deCandolle for J. Müller 1876; e, f, and g: [blank]; h: Florence Roy. Acad. Sr. Parlatore Nov. 1875; i: J. K. 1. I have now been able to determine that sets were finally sent to British Museum (21 specimens), Uppsala (UPS) (23 specimens), Stockholm (S) (20 specimens sent in 1879), Geneva (G) (11 specimens), Vienna (W) (5 specimens), and Paris (PC) (10 specimens) (numbers for G. PC, and W are counts of only type duplicates). These institutions would account for most of the blanks in the notebook. As I will show in the species lists under specimens examined, these duplicates are sometimes mixtures and the determinations not always trustworthy.

The collections at Peradeniya are extremely important since 175 of the total 196 Leighton species, including most of the types, are represented there. It is unusual, even today, for tropical herbaria to have duplicates of lichens of their own country collected and determined by lichenologists from America and Europe. The only species missing are numbers 3, 8, 11, 33, 34, 38, 42, 53, 57, 60, 62, 76, 101, 109, 125, 127–129, 173, and 191, as enumerated in Leighton's publication.

Thwaites apparently kept no field books for the C. L. number series which was reserved for lichens. Taking the Thelotremataceae, however, we find that the first C. L. collection number was 5 and the last 284. The last number in BM, however, is 175, and I am not sure how or when the C. L. numbers between 175 and 284, now filed on the same sheets in Peradeniya with numbers 5–175, were identified. In general, the correspondence between the PDA and BM collections, where both are accounted for, is surprisingly good. There are very few cases of erroneous mixtures such as *Thelotrema exanthismocarpum* (C. L. 97), which is represented in PDA by a misidentified *'Ocellularia' stictidea* (C. L. 200) (= *Conotrema*).

The Almquist collections

In summarizing the historical development of research on the lichens of Sri Lanka, one cannot overlook a small but important collection of thelotremes made by Almquist, the famous Swedish explorer. He visited Peradeniya in December 1879. Thwaites, extremely pleased to have a distinguished visitor in this isolated post, took him on trips to the Peradeniya area, Point de Galle, a coastal area in southernmost Sri Lanka, and Pidurutalagala (Pedrotallegalle), the highest point on the island. I was able to climb this mountain in 1978 on the same well-worn trail used by Almquist and recollect some of the species he found.

The Almquist collections, including those from Japan and other countries visited during the Vega expedition, were sent to Nylander for identification. This material formed the basis for Nylander's final scientific work, 'Lichenes Ceylonenses', published posthumously in 1900. The original specimens are now preserved in Stockholm with fragments in Nylander's herbarium at Helsinki. In the article Nylander lists only two species described by Leighton, *Asteristion erumpens* (= *Thelotrema platycarpum)* and *Thelotrema albidiforme* (redetermined correctly as *T. porinoides*), both of which Leighton had sent him for comment. Seven other species were collected by Almquist. When later preparing his own article on Ceylon lichens based on Almqujst's collections, Nylander (1900: 26) admitted that his list was much poorer than Leighton's and at the same time complained indirectly that he was not able to lay his hands on Leighton's specimens, unfortunate in his mind since he had doubts about the identifications. This is a curious reprimand since Leighton had sent him 23 Thwaites specimens of Thelotremataceae for comment in 1868–69. Representatives of the other families were also sent, although in lesser numbers.

Recent collections

Following Thwaites by almost 70 years, A. H. G. Alston spent the years 1926–31 in Sri Lanka, collecting widely and adding plant specimens, including a few lichens, to the Peradeniya herbarium (Crabbe, 1960). He wrote the Kandy flora (with a listing *Thelotrema lepadizum*) (Alston, 1938), a supplement to Trimen's Handbook, and unpublished taxonomic treatments of Ceylon bryophytes, algae, and lichens. The treatment for lichens, now on file in the cryptogamic library of the British Museum, is essentially a compilation of Leighton's lichen flora.

Other recent collecting has been done incidentally under the Smithsonian Institutions' Flora of Ceylon Project from 1970–1976, mostly by Louis Wheeler in drier lowland areas. His specimens are preserved in Peradeniya and the Smithsonian Institution.

Among professional lichenologists, I know of a brief visit in 1975 by Rolf Santesson and Roland Moberg, who together collected about 10 specimens of Thelotremataceae, mostly in the Horton Plains area. These are in Uppsala with some duplicates in the Smithsonian (US). My own excursions are given below under 'Collecting localities' (p. 247).

Other lichenologists and bryologists have probably collected the Thelotremataceae on Sri Lanka but I have not attempted to examine their collections.

Morphology: structural characters

We are still not sure what value should be attached to structural characters in the taxonomy of crustose lichens. Foliose lichens have great diversity not only in cortical structure, which lichenologists are only now taking into serious consideration, but also in vegetative structures such as rhizines and diaspores such as isidia and soredia, which have long been accepted. Magnusson (1939: 10), the acknowledged master of crustose lichens, placed little value on cortical structure since 'the real arrangement of the hyphae is difficult to observe in hand-cut sections and certainly is of little practical importance, irrespective of the trustworthiness of this character'. It can indeed be difficult to interpret cortical organization in the Thelotremataceae and other crustose lichens with a light microscope (see Fig. 1) because the tissues are much denser than corresponding ones in macrolichens, but at the same time no character should be rejected simply because of difficulties in observing it.

I have approached this problem by studying and comparing cross sections with both the light microscope and the scanning electron microscope, using the same specimen face when sectioning. Specimen preparation for the scanning microscope follows Hale (1973*a*: 2). The results are not claimed to be final but will hopefully point out interesting avenues for future research in the family.

Hypophloeodal species

According to various authors, hypophloeodal species lack a clearcut cortex, the algae being superficial or dispersed among the outer periderm layers. The medulla is mainly located among periderm cells. The scanning electron microscope supports this description in large part (Figs 2a, b; Hale, 1974*a*: 6, Fig 4), and the following species in Sri Lanka can be called hypophloeodal: *Ocellularia leucomelaena, O. meiosperma, O. meiospermoides, O. melanotremata, O. tenuis, Thelotrema alborosellum, T. coccineum, T. colobicum, T.*

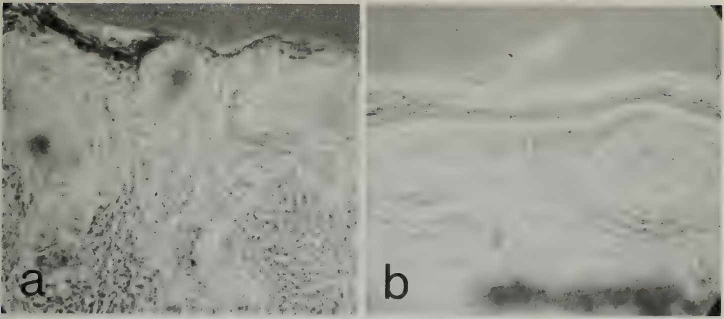

Fig. 1 Thallus in the Thelotremataceae viewed with a light microscope. (a) Cross section of *Myriotrema multicavum* (Hale 46 150, × 500) showing the columnar medulla and crystals. (b) Exfoliating cortex of *M. terebrans* (Hale 47 202, × 500) with crystal inclusions.

dilatatum, T. lacteum, T. lepadinum, T. leprocarpoides, T. monosporum, T. nostalgicum, T. novae-zelandiae, T. patens, T. phlyctidioides, T. porinoides, T. subpatens, T. waasii, and *T. weberi.* No species of *Myriotrema* are hypophloeodal although *M. decorticatum* has extensive decorticated areas.

The algal layer in these species may actually persist intact among a thin, non-corticated layer of 'medullary' hyphae that covers the plant body as a wispy white colouration. In addition, the medullary hyphae are not only intercellular in the periderm, but also intracellular (Hale, 1974*a*: 6, Fig. 4d; also Fig. 2c). One soon realizes that hypophloeodal species may have no more medullary hyphae growing below the periderm than do the epiphloeodal (corticate) species. The term non-corticate approximates the true anatomical condition of these lichens most accurately, although a few distinctly thalloid species (as *Myriotrema glaucescens*) to be mentioned below may also lack a cortex.

Obviously much work remains to be done before a full understanding of hypophloeodal species is achieved, not only in terms of morphological development but also correlations with other characters. For example, non-corticate species have an unusually high frequency of stictic acid or no substances. Furthermore, they lack completely psoromic acid and other substances often found in the corticate (epiphloeodal) species. These few observations suggest that lack of a cortex is a primitive character.

Epiphloeodal species

Cortex

Epiphloeodal species have a distinct cortex, algal layer, and medulla (Fig. 2d). The scanning electron microscope shows more variation than one would expect from the usual hand drawings of the species (see Redinger, 1936, or Salisbury, 1978). Basically, the cortex consists of a highly agglutinated, continuous layer 2–5 cells (8–15 μm) thick, the individual cells lying more or less randomly in a horizontal plane, their walls heavily gelatinized. Salisbury's term 'cartilaginous' seems quite appropriate (see Figs 1b, 6a, b).

On closer inspection, one can detect subtle differences in the degree of gelatinization and density of packing, obviously characters which may intergrade and require subjective judgement. For example, the following species in Sri Lanka have rather loosely packed, individually recognizable cells in the cortex: *Myriotrema anamalaiense, M. andamanicum, M. mastarion, M. porinaceum, M. thwaitesii, Ocellularia ascidioidea, O. chonestoma* (Fig. 3c), *O. dolichotata, O. eumorpha, O. neopertusariiformis, O. nylanderiana, O. orthomastia,*

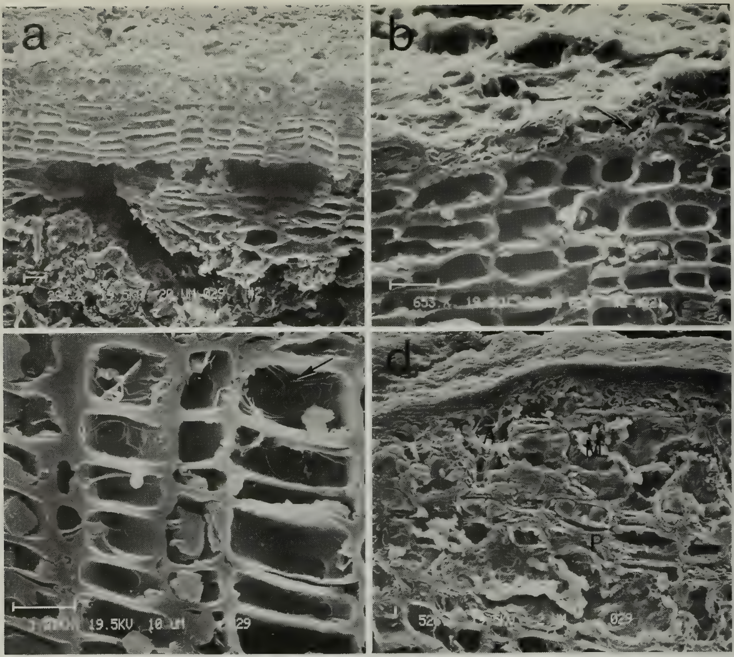

Fig. 2 Thallus structure in the Thelotremataceae viewed with the scanning electron microscope. (a) Low power view of cross section of a hypophloeodal species (*Thelotrema waasii,* Hale 51 175). (b) Cross section of a hypophloeodal species showing patches of medullary hyphae (arrow) on periderm surface (*T. dilatatum*, Hale 46 218). (c) Enlargement of periderm cells to show intracellular hyphae (arrow) (*Ocellularia kanneliyensis*, Hale 46 213). (d) Low power view of cross section of an epiphloeodal species (*O. perforata*, Hale 47 010) showing cortex (C), algal layer (A), medulla with crystals (M), and periderm (P).

O. pertusariiformis, O. rhicnopora, O. triglyphica, Thelotrema imperfectum (Fig. 3a), and *T. nureliyum.* The surface of some of these species may appear to be irregularly pored (Fig. 3c).

A second group of species has more heavily gelatinized, compressed cells in the cortex with only the small lumina suggesting outlines of hyphal organization: *Myriotrema elachistoteron, M. granulosum, M. microporum, M. nuwarense, Ocellularia aurata, O. diacida, O. exuta, O. kanneliyensis, O. keralensis, O. lirelliformis, O. monosporoides, O. neocavata, O. sticticans, O. thelotremoides, Thelotrema aggregatum, T. astroideum, T. dissultum, T. kamatii, T. leprieurii, T. platycarpoides, T. platycarpum, T. pseudoexanthismocarpum,* and *T. pulvereodiscum.* The surface of these species is usually featureless and non-pored under the scanning electron microscope.

A third group of species, comprising the majority of those in the family, is corticate but differs from the species mentioned above in having aculeate hyphae on the surface. I first

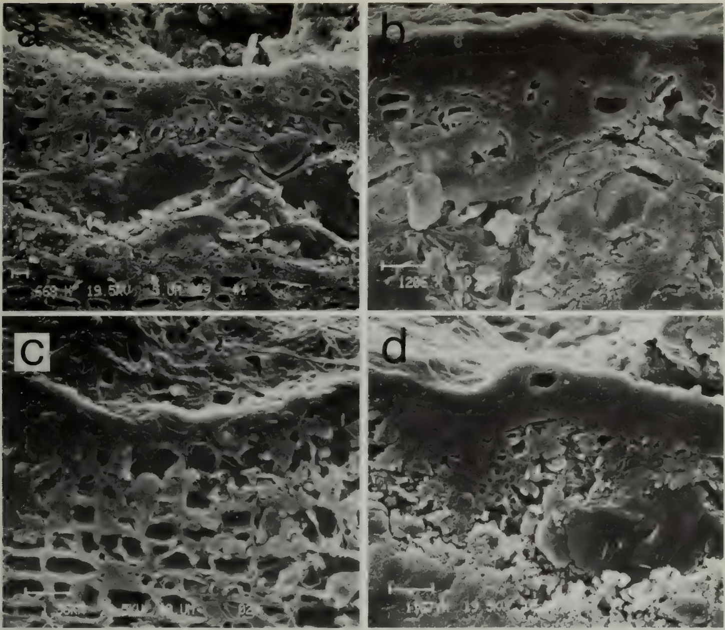

Fig. 3 Cortical structure of the Thelotremataceae viewed with a scanning electron microscope. (a) Loosely organized cellular cortex of *Thelotrema imperfectum* (Hale 46 338). (b) Dense cellular cortex of *Myriotrema album* (Hale 4 171). (c) Loosely organized, irregularly pored cortex of *Ocellularia chonestoma* (Hale 46 344). (d) Dense cellular cortex of *O. crassa* with large crystal inclusions (Hale 51 210).

discovered these peculiar hyphae in some West Indian species (Hale, 1974*a*: 5, Fig. 3), using the scanning electron microscope, and can now add more details from the larger material in Sri Lanka. Aculeate hyphae are unicellular, non-gelatinized, and erect and seem to fade into the main polysaccharide cortical surface (Fig. 4a). They are far too delicate and translucent to be seen with a light microscope and usually collapse after vacuum treatment needed in electron microscope preparation.

There are three major groups of species with aculeate hyphae: (1) species with a loosely organized cortex (*Ocellularia chonestoma, O. dolichotata,* and *O. pertusariiformis* already mentioned above); (2) species with a dense, continuous cortex (*Myriotrema albocinctum, M. eminens, M. fissurinum, M. hartii, M. olivaceum, M. protoalbum, Ocellularia crassa* (Fig. 3d), *O. fissa, O. perforata, O. punctulata,* and *Thelotrema scabiomarginatum*); and (3) species with a dense cortex which splits into sheets or layers and may exfoliate at the surface (*Myriotrema album* (Fig. 3b), *M. cinereoglaucescens, M. clandestinum, M. costaricense, M. desquamans, M. fluorescens, M. frondosum, M. glaucophaenum, M. masonhalei, M. microstomum, M. minutum, M. polytretum, M. santessonii, M. subconforme, M. terebrans, M. terebratulum, Ocellularia albomaculata, O. croceopora, O. emersa, O. lankaensis, O.*

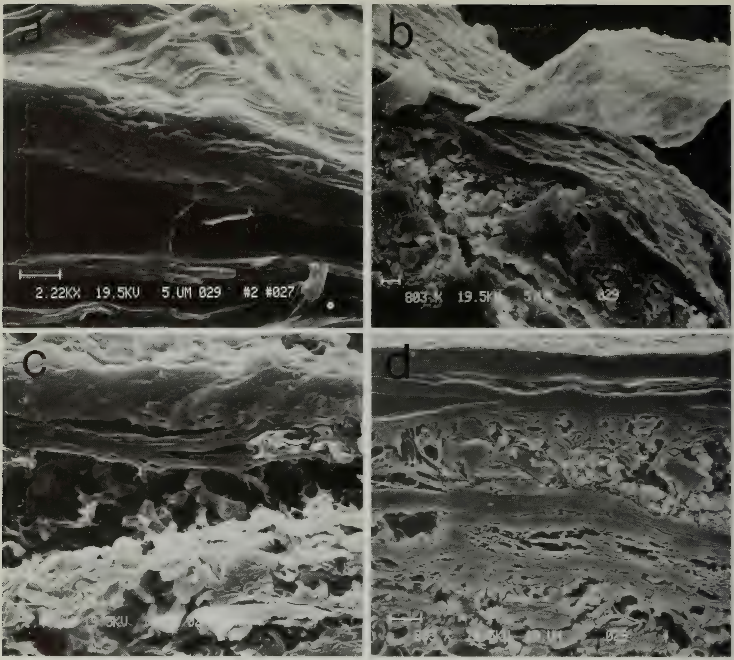

Fig. 4 Cortical structure of the Thelotremataceae viewed with the scanning electron microscope. (a) Splitting cortex and aculeate hyphae of *Myriotrema glaucophaenum* (Hale 47 062). (b) Exfoliating sheet of *Ocellularia emersa* (Hale 51 068). (c) Internally splitting cortex of *Myriotrema fluorescens* (Hale 47 152). (d) Internally splitting cortex of *Ocellularia croceopora* (Hale 46 186) showing incorporation of sheets into the medulla.

marivelensis, O. massalongoi, O. papillata, O. pluripora, O. polillensis, O. rassagala, O. subsimilis, Thelotrema magnificum, T. piluliferum, and *T. platysporum*).

Exfoliation of the cortex was probably first observed by Müller Argoviensis when he described *Anthracothecium (Myriotrema) desquamans* as having 'plaguliformi desquamans'. Using a light microscope one can see the cortex splitting into thin sheets which may curl up and peel off the surface (Fig. 1b). The cortex may also split internally, giving rise in extreme cases to alternating, stratified layers of cortex and medulla, as in *Ocellularia croceopora* (Fig. 4d). These layers may be only one cell layer thick or 20 μm or more, regenerating from below as sheets subdivide or peel off. The constant occurrence of aculeate hyphae in species with an exfoliating cortex suggests that these hyphae initiate or promote the splitting process in some way since they can be seen on the surface of newly exfoliating sheets (Fig. 4b). The same phenomenon occurs in the Graphidaceae (Wirth & Hale, 1978) and will surely be discovered in other crustose groups.

There is a high degree of correlation between cortical structure and chemistry, although I have not tested this statistically. Species with hypoprotocetraric acid or no substances appear

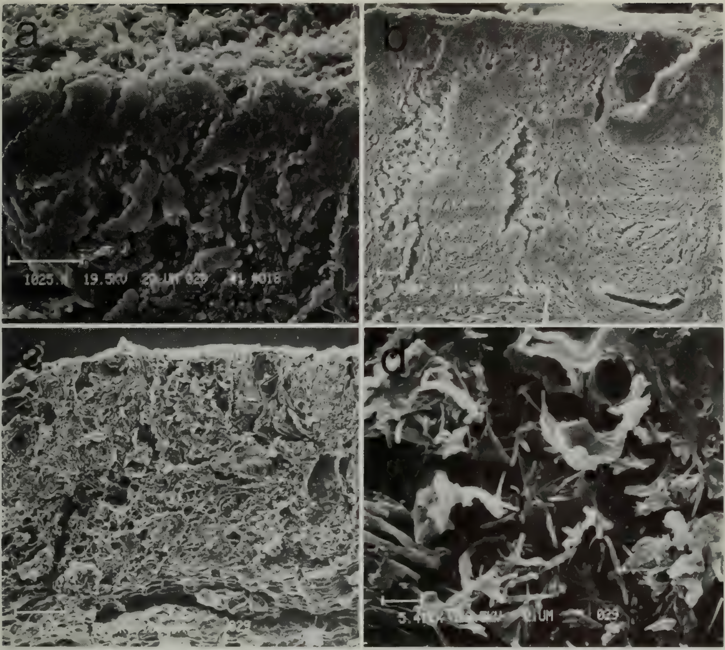

Fig. 5 Medullary structure of the Thelotremataceae viewed with the scanning electron microscope. (a) Upper medullary area of *Myriotrema glaucescens* (Hale 50 334) showing massed suberect hyphae at the surface. (b) Columnar cortex of *M. microporum* (Hale 46 271). (c) Crystal-filled medulla of *M. multicavum* (Hale 46 150) (compare with Fig. 1a). (d) Crystals of psoromic acid on medullary hyphae of *Ocellularia lankaensis* (Hale 51 008).

to have a more loosely organized cortex and rarer occurrence of aculeate hyphae than expected. The correlation between aculeate hyphae, cortical splitting, and chemistry is more striking. All 23 species in Sri lanka with psoromic acid, excepting *Myriotrema andamanicum* and *M. mastarion,* have aculeate hyphae and a high frequency of cortical splitting. More exhaustive examination of all species in the family will undoubtedly reveal additional correlations.

Algal layer

The mycobiont in the Thelotremataceae is *Trentepohlia.* Within the thallus this alga forms unicellular spheres evenly distributed in a layer 2–4 cells thick (10–30 μm). In many species, the layer is interrupted by intrusions of oxalate crystals. When the medulla is missing, the algal layer lies on and may be partly dispersed in the periderm.

Medulla

The medulla of epiphloeodal species varies considerably in thickness. Even in the same plant it may be virtually absent—the algae resting directly on the periderm—or as much as 60–100 μm thick. The medulla is modified by the bark substratum in many ways. A uniform layer of medulla forms over a hard periderm, but if the periderm disintegrates easily the medulla may not only penetrate deeply in periderm fissures but even incorporate layers of bark cells.

Many species of the Thelotremataceae produce oxalate crystals (Figs 1a, 5c), which are so abundant in some (e.g. *Myriotrema multicavum*) (Fig. 5c) that cohesion of the hyphae is broken and the thallus abrades and crumbles easily. The origin of these crystals is uncertain but from my observations they appear to be produced by the medullary hyphae and are species specific. They are probably a waste product, stimulated by the very close contact between the medulla and periderm. They may even have a conceivable function in magnifying the light rays which pass through the cortex and become dispersed to the algae closely surrounding the crystals. Species containing psoromic acid may have additional conspicuous masses of acid crystals on the hyphae (Fig. 5d).

There is, finally, an unusual, highly developed medulla in a small group of species, all in the genus *Myriotrema*. It consists of vertically oriented, cellular blocks of tissue 200–1000 μm thick (see Hale, 1974*a*: 3, Fig. 1d) with algae oriented between the vertical arrays. One such species in Sri Lanka, *Myriotrema microporum*, has a well developed cortex (Fig. 5b), but the others in this group, *M. compunctum*, *M. glaucescens* (Fig. 5a), *M. multicavum*, and *M. wightii* all lack a cortex. The surface consists of knobby, packed medullary hyphae sometimes covered with an irregular, pored polysaccharide sheet. I do not believe, however, this can be compared with the epicortex of foliose lichens.

In conclusion, I feel that structural characters in crustose lichens, as exemplified by the Thelotremataceae, are sufficiently distinctive and constant to play some role in the taxonomy. However, we have barely begun to explore the nature and range of variation of these structures with the new analytical tools available; future workers will be in a better position to evaluate them.

Apothecial characters

The exciple

Over 100 years ago Tuckerman (1864: 270) stated that 'it will not be easy to found any subdivision of (*Thelotrema*) on the presence or absence of the interior exciple'. There has, indeed, been much controversy and uncertainty about the usefulness of apothecial characters in the family even up to the present time. The only developmental study is one by Letrouit-Galinou (1966) for *Thelotrema lepadinum*, and many of our conclusions on the other 450 species in the family must be based on far less satisfactory evidence.

To summarize what we do know about apothecial characters, one of the most characteristic features of the family is the periphysoid-bearing exciple, constant for the genus *Thelotrema*. This exciple arises from the base of the hymenium and is covered with periphysoids on the inner surface (Salisbury, 1972*a*). Periphysoids are short paraphyses-like hyphae oriented at right angles to the paraphyses of the hymenium (Fig. 6c), similar to the better known periphyses of pyrenocarpous lichens (Henssen & Jahns, 1974). Redinger (1936) overlooked them completely in his otherwise careful studies of the family in Brazil. They were apparently first recognized by Zahlbruckner (1941: 16) in *Thelotrema periphysatum* Zahlbr. (= *T. lepadinum*) and soon thereafter by Magnusson (Magnusson & Zahlbruckner, 1944: 53) in *Thelotrema gibbosum* Magn. (= *T. piluliferum* Tuck.).

Another typically thelotremoid character is the carbonized columella. While I know of no developmental studies on this structure, Redinger (1936: 7) found that the ascogonial initials ('die Primordien der Apothecien') of columellate species originate in the periderm at a depth of 3–5 cells. He surmised that the columella functions as a 'Rammbock', which breaches this layer of bark cells as the apothecia mature and reach the surface. Although this simplistic explanation may be close to the truth, a number of *Myriotrema* species (e.g. *M.*

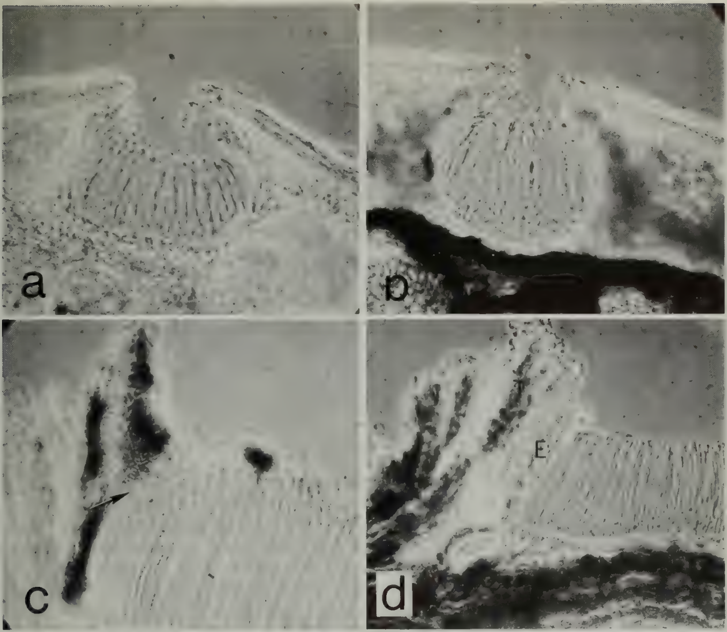

Fig. 6 Apothecial structure in the Thelotremataceae viewed with a light microscope. (a) Immersed apothecium of *Myriotrema album* (Hale 46 171). (b) Immersed apothecium of *M. minutum* (Hale 50 315). (c) Exciple with periphysoids (arrow) in *Thelotrema nureliyum* (Hale 50 292). (d) Thalline rim (T) and partially fused exciple (E) of *T. subpatens* (Hale 46 208) (all about × 500).

andamanicum and *M. mastarion*) have deeply embedded apothecia capable of reaching the surface without a columella. In any event columellate species always have a fused, carbonized, exciple lacking periphysoids. All species of *Ocellularia,* as circumscribed in this revision, have a carbonized exciple and a high proportion of them have a columella. A few species develop a broad, divided, or reticulate columella, often with an open disc. Vainio (1921: 184) recognized these in separate genus, *Rhabdodiscus* (= *Stegobolus* Mont.).

A third major group of species, all in *Myriotrema,* have a fused, noncarbonized exciple without periphysoids (Figs 6a, b). The exciple is colourless or pale yellowish to reddish brown but may be poorly developed to lacking laterally.

There is considerable variation in the development of the thalline wall. It is perhaps most conspicuous in the genus *Thelotrema,* where many species have a nearly erect rim and gaping pore (see Figs 7e, f). Other species of *Thelotrema* have an erect to strongly recurved and split wall (see Figs 9h, 10b), so unique that Leighton described a new genus *Asteristion* on the basis of one of them. I have called these apothecia chroodiscoid (Hale, 1978*a*: 2), deriving the term from the well-known genus name *Chroodiscus* (= *Thelotrema*).

Ocellularia has a well-developed thalline wall described as incurved, resulting in a constricted, often rimmed pore. *Myriotrema,* on the other hand, generally has a weakly developed wall or none at all, since many of the species have apothecia completely immersed in the medulla.

Spore characters

The family Thelotremataceae is characterized by four basic spore types differentiated by colour (colourless or brown) and septation (transversely septate or muriform). There is surprisingly little intergradation between them. In most cases, abnormal darkening of otherwise colourless spores seems to result from senescence. *Ocellularia patwardhanii* Hale (Hale, 1978*b*: 379), *O. rhodostroma* (Mont.) Zahlbr., and *O. subcavata* (Nyl.) Zahlbr. (Hale, 1974*a*: 28) may all have some brown spores at an evidently moribund stage. A few species such as *Ocellularia monosporoides* (Nyl.) Hale have predominantly colourless spores which turn brownish tardily at maturity. As for septation, a very few species with transversely septate spores may develop a few longitudinal septa in the end cells, as in *Thelotrema pidurutalagalum.* Abnormal spore pigmentation and septation are also known in the Graphidaceae (Wirth & Hale, 1978: 2).

Some lichenologists have placed considerable emphasis on the shape of cell lumina in the family. For example, most species with 4-celled spores have thickened walls, giving a lenticular appearance. Densely muriform spores, as in *Thelotrema monosporum,* have more thin-walled, cubical cells. Obviously a definitive determination of shape of lumina will require much more detailed investigation.

Generic classification

Generic and subgeneric divisions of the Thelotremataceae have varied widely with different authors. Acharius proposed the first genus, *Thelotrema,* which included only 15 species in his lifetime. He was followed by Fée in 1824, who examined a wider range of specimens and had a greater appreciation of microscopic characters, recognizing three genera, *Thelotrema* and two others described as new, *Ascidium* and *Myriotrema.* These names were no sooner published than G. F. W. Meyer in 1825 added three more, *Ocellularia* (later conserved against *Ascidium*), *Antrocarpum* (based on *Lichen lepadinus* Ach. and therefore a synonym of *Thelotrema*), and *Porophora* (a superfluous name for *Ascidium*).

Additional names were proposed by Massalongo, Montagne, Hampe, and others in the 19th century, as will be seen in the lists of generic synonymy in the species list below, but few were ever adopted in practice. Nylander, the most active worker in the Thelotremataceae, began his studies by recognizing *Ascidium* and *Thelotrema* but soon reverted to one genus, *Thelotrema,* and during his long career from 1858 to 1900 finally ignored all other names, making no contributions at all to generic concepts in the family. He subdivided the species into four groups differing principally in spore colour, size, and septation (Nylander, 1862). His countryman, Vainio, also classified all species in *Thelotrema,* excepting the reticulate-columellate species, segregated as *Rhabdodiscus.*

Müller Argoviensis, Nylander's contemporary but certainly not his admirer, employed spore characters (colour and septation) to divide the family into four genera, *Ocellularia* (colourless, transversely septate), *Phaeotrema* (brown, transversely septate), *Thelotrema* (colourless, muriform), and *Leptotrema* (brown, muriform). This system is easy to apply since spore characters are readily determined with a light microscope. It was reinforced when Zahlbruckner adopted it in his *Catalogus Lichenum Universalis* and Redinger (1936) followed it in his important study of the family in Brazil. Further subdivisions of the spore genera were founded on various macroscopic characters such as a degree of emergence, presence of a columella, etc., with little consistency, but as a result each genus contained essentially similar, parallel series of sections based on gross apothecial morphology. Species with identical apothecial structure were often as not artificially dispersed in different genera. This awkward classification deserves no further elaboration here; it is summarized by Redinger (1936) in considerable detail.

Among recent lichenologists Salisbury (1971*a*) has vigorously challenged the continued use of spore genera in the Thelotremataceae. He rejects spores categorically and revives a classification based solely on excipular characters, recognizing one genus, *Thelotrema*, divided into three sections, *Thelotrema* (exciple colourless, with periphysoids), *Myriotrema* (exciple colourless or brownish, without periphysoids), and *Ascidium* (exciple carbonized, columella often present). These sections have the same circumscription as Fée's three genera, *Thelotrema, Myriotrema,* and *Ascidium* (= *Ocellularia*).

Although I used the spore genera in my previous studies of the family (Hale, 1974*a*, 1978*a*), I have come to agree with Salisbury that excipular and other apothecial characters represent more natural traits than do spores. Indeed, spores, which so long served to separate genera, can be used to undermine them with equal cogency. For example, there are a number of species groups which have identical thallus morphology, excipular structure, and chemistry but spores of different colour or septation. A good case is the *Thelotrema lepadinum-Phaeotrema lacteum-Leptotrema monosporum* complex, three hypophloeodal species with a free, periphysoid-bearing exciple which manifestly associates them in one genus, *Thelotrema*. I had previously called these sporomorphs (Wirth & Hale, 1978: 2) in an attempt to rationalize their existence in spore genera.

Another example is the reticulate-columellate series *Ocellularia emersa-Phaeotrema virens-Leptotrema crassum,* which have identical external morphology, carbonized exciple, and chemistry (psoromic acid). Their natural relationship is better expressed by placing them in one genus and regarding spore differences as a species character. Other examples will be cited below in the species list. They are not numerous, about 30 of the 450 species at the world level falling into this category, but more than adequately damage the credibility of spore-based genera.

Having accepted excipular structures as a natural generic base, one soon realizes, however, that the use of one genus (*Thelotrema*) for 450 species is an unwieldy solution, especially since three well-delineated groups can be recognized. I have proposed to recognize Fée's three genera for the reasons given below (see also Hale, 1980).

The classic genus *Thelotrema* can be characterized by the constant presence of periphysoids and the frequent occurrence of a free (detached) exciple. Salisbury (1972*a*) assigned about 20 species here (as section *Thelotrema*) after studying some 200 type specimens. According to my own results, based on a study of over 350 types and much newly collected material, there are about 100 species of *Thelotrema,* of which 32 occur in Sri Lanka.

A preliminary survey of the 100 species of *Thelotrema* brought out some interesting and, I believe, significant correlations with morphology and chemistry. For example, about 33 species of *Thelotrema* at the world level lack a cortex, that is, are hypophloeodal. This suggests a high degree of primitiveness in the genus. The species are also distinctive in having a gaping pore, referred to as 'apothecia excavata' by Fée. In fact, species in Salisbury's section *Thelotrema,* '*platycarpum*' group, have an open disc surrounded by a conspicuous reflexed thalline rim, unique to the genus (Salisbury, 1972*b*: 281).

The chemistry of *Thelotrema* is particularly impoverished in comparison with *Myriotrema* and *Ocellularia.* Sixty of the species contain no lichen substances at all, a very high proportion compared to the other two genera. About 30 of the remaining species contain stictic acid and 14 others have fumarprotocetraric acid, hypoprotocetraric acid, protocetraric acid, norstictic acid, or salazinic acid. The most striking feature is the rarity of psoromic acid, otherwise the most common substance in the family. It occurs only in a small group of species, *T. cryptotrema* Nyl., *T. piluliferum* Tuck., *T. platysporum* Harm., *T. saxicola* Vainio, and *T. sphinctrinellum* Nyl., which do not, in any event, fit comfortably in the genus.

Myriotrema, the second largest genus, is represented by nearly 150 species, 37 of them in Sri Lanka. Fée based it on immersed apothecia and the easily distinguished, thick cortex and medulla as seen in *M. olivaceum.* One of the unusual features of the genus is actually the high percentage of species with small immersed apothecia (0·2–0·4 mm in diameter) and small spores. Those with emergent or raised apothecia are classified by Salisbury in *Thelotrema* section *Myriotrema,* the '*T. bahianum*' group, which has an incurved thalline wall. The exciple in all the species is fused and colourless to brown, rarely lacking laterally.

All species of *Myriotrema* have a distinct, often relatively thick medulla, and excepting *M. glaucescens, M. multicava,* and *M. wightii,* a distinct cortex, which is frequently aculeate and exfoliating as in *Ocellularia.* There are no hypophloeodal species.

The chemistry of *Myriotrema* is nearly as varied as that of *Ocellularia.* Psoromic acid occurs in 50 (about 33%) of the 150 species known at the world level. Stictic acid is relatively more abundant (22 species) than in *Ocellularia,* but protocetraric acid (11 species) and hypoprotocetraric acid (4 species) less abundant.

Ocellularia, treated by Salisbury as *Thelotrema* section *Ascidium,* is the largest genus in the family with about 200 species, of which 41 occur in Sri Lanka. It can be easily recognized by the fused, carbonized exciple, a trait which Montagne (1856: 364) used to characterize *Ascidium,* and the frequent occurrence of a central columella. While the apothecia vary greatly in size and emergence, the pore is usually constricted and distinct with an incurved thalline rim. Fée himself had emphasized the marginate, depressed pore when describing *Ascidium.*

The cortical structure of *Ocellularia* is as complex as that in *Myriotrema.* Only about 10 species lack a cortex. The corticate ones often have aculeate hyphae on the surface and exfoliation or splitting.

The chemical profile of *Ocellularia* is very rich. There are many species, about 50 of the presently known 200, with psoromic acid, 25 with protocetraric acid, and 20 with hypoprotocetraric acid. Only about 50 species (25%) lack lichen substances, and only 11 have stictic acid. When the species are divided into spore groups, the only noteworthy observation is that 12 species with transversely septate colourless spores have the 'cinchonarum' unknown; only one muriform species has it. Otherwise the four spore types appear to have similar frequencies of each acid insofar as statistically significant numbers of species are compared.

Family classification

The family Thelotremataceae is readily identified by the pored apothecium. Santesson (1952: 306) briefly referred to the family in his exhaustive study of the foliicolous lichens. He felt that the family is closely related to the Graphidaceae, still a commonly held perception. Vězda (1966) studied a number of related genera and suggested affinities with the Diploschistaceae without making any formal proposals to combine them, this being done recently by Henssen & Jahns (1973: 374). Using the presence of periphysoids as a fundamental character, Vězda transferred *Ramonia* and *Gloeolecta* from the Gyalectaceae and placed them in the Thelotremataceae. Finally, Gilenstam (1969) places *Thelotrema, Ocellularia, Phaeotrema,* and *Leptotrema* along with the Graphidaceae, *Diploschistes,* and *Conotrema* under the order Ostropales without specifying a family breakdown. He pointed out a close relationship to *Stictis,* a periphysoid-bearing fungal genus, and a recent monograph on the ostropalean fungi by Sherwood (1977) confirms this.

Zahlbruckner (1923) included *Tremotylium* Nyl. in the Thelotremataceae even though Vainio (1921: 184) had already discovered that *T. angolense* Nyl., the type of the genus, is probably an *Anthracothecium,* since it has branched, anastomosing paraphyses. I would follow Santesson (1952) in transferring *Gyrostomum,* also placed in the Thelotremataceae by Zahlbruckner, to the Graphidaceae, and I would add *Tremotylium sprucei* Müll. Arg., which is not related to *Tremotylium.* The status of *Polystroma* Clemente, a very rare South American genus, is unclear at this time.

The family Thelotremataceae as conceived now includes seven genera: *Conotrema, Diploschistes, Gloeolecta, Myriotrema, Ocellularia, Ramonia* and *Thelotrema.* It will almost certainly be expanded when more definitive studies on the Gyalectaceae are completed.

Chemistry

As I earlier found in my studies of the Thelotremataceae in Dominica and Panama, the chemistry of this family is rich and diversified. The various species contain depsides and depsidones which can be determined easily with thin-layer chromatography [t.l.c.]. In my opinion, a knowledge of the chemical constituents is essential both for routine species identification and for a fuller understanding of speciation and evolution in the family. One would be seriously disadvantaged without this information.

The lichen substances found in the 110 species from Sri Lanka are listed below alphabetically with the species in which they occur. All specimens were examined with t.l.c. using Merck F-254 precoated plates in two solvent systems (benzene-dioxane-acetic acid and hexane-ether-formic acid) and in a third (n-butanol-acetone-water) when distinguishing fumarprotocetraric acid and protocetraric acid. Plates were examined under shortwave ultraviolet, sprayed with 10% H_2SO_4, and heated at 100°C to develop the colours. Fuller descriptions of problems in identification or the unknown compounds will be found in the list of species.

Constictic acid (see stictic acid).

Fumarprotocetraric acid: *Myriotrema microstomum* (with traces of protocetraric acid), *M. minutum*, *Ocellularia thelotremoides* (with nearly equal amounts of protocetraric acid), and *Thelotrema nostalgicum*.

Hypoprotocetraric acid (usually with 4-0-demethylnotatic acid): *Ocellularia eumorpha*, *O. kanneliyensis*, *O. neopertusariiformis*, and *O. triglyphica*.

Lichexanthone: *Myriotrema fluorescens*.

Norpsoromic acid: See psoromic acid.

Norstictic acid: *Myriotrema compunctum* (with stictic acid), *M. porinaceum*, and *Thelotrema weberi*.

Protocetraric acid: *Myriotrema microstomum* (in traces with fumarprotocetraric acid), *Ocellularia aurata*, *O. perforata*, *O. subsimilis*, and *O. thelotremoides* (with equal amounts of fumarprotocetraric acid).

Psoromic acid (often with norpsoromic acid): *Myriotrema andamanicum*, *M. costaricense*, *M. frondosum*, *M. glaucophaenum*, *M. hartii*, *M. masonhalei*, *M. mastarion*, *M. microporum*, *M. minutulum*, *M. multicavum*, *M. rugiferum*, *M. terebratulum*, *Ocellularia crassa*, *O. emersa*, *O. exuta*, *O. fissa*, *O. lankaensis*, *O. marivelensis*, *O. pluripora*, *O. polillensis*, *O. rassagala*, *Thelotrema piluliferum*, and *T. platysporum*.

Salazinic acid: *Ocellularia massalongoi*.

Stictic acid (often with constictic acid and associated unknowns A_1 and A_2): *Myriotrema anamalaiense*, *M. compunctum* (with norstictic acid), *M. decorticatum*, *M. desquamans*, *M. elachistoteron*, *M. eminens*, *M. fissurinum*, *M. glaucescens*, *M. nuwarense*, *M. santessonii*, *M. terebrans*, *Ocellularia melanotremata*, *O. pyrenuloides*, *O. sticticans*, *Thelotrema dilatatum*, *T. dissultum*, *T. novae-zelandiae*, *T. patens*, *T. phlyctidioides*, *T. platycarpoides*, *T. platycarpum*, *T. porinoides*, and *T. pulvereodiscum*.

No lichen substances present (anthraquinones may be present; see below): *Myriotrema album*, *M. albocinctum*, *M. cinereoglaucescens*, *M. protoalbum*, *M. subconforme*, *M. wightii*, *Ocellularia albomaculata*, *O. ascidioidea*, *O. dolichotata*, *O. keralensis*, *O. leucomelaena*, *O. lirelliformis*, *O. meiosperma*, *O. meiospermoides*, *O. monosporoides*, *O. orthomastia*, *O. papillata*, *O. rhicnopora*, *O. tenuis*, *Thelotrema aggregatum*, *T. alborosellum*, *T. astroideum*, *T. colobicum*, *T. imperfectum*, *T. kamatii*, *T. lacteum*, *T. lepadinum*, *T. leprieurii*, *T. leprocarpoides*, *T. magnificum*, *T. monosporum*, *T. nureliyum*, *T. pidurutalagalum*, *T. pseudoexanthismocarpum*, *T. scabiomarginatum*, *T. subpatens*, and *T. waasii*.

K+ purple anthraquinones: *Myriotrema wightii* (medullary), *Ocellularia punctulata* (medullary), *Thelotrema coccineum* (epithelial), and *T. magnificum* (epithelial).

K+ yellow-orange pigments: *Ocellularia aurata* (epithelial).

'Cinchonarum' unknown (P+ red-orange): *Ocellularia neocavata*, *O. punctulata*.

'Chonestoma' unknown (with upper 'olivacea' unknown) (P−): *Ocellularia chonestoma*, *O. croceopora*, *O. nylanderiana*.

'Diacida' unknown (P+ yellow-orange): *Ocellularia diacida*.

'Leightonii' unknown (P+ orange-red): *Myriotrema granulosum*.

'Olivacea' unknown (P−): *Myriotrema olivaceum*.

'Pertusariiformis' unknown (P−): *Ocellularia pertusariiformis.*
'Platysporum' unknown (P+ red): *Thelotrema platysporum.*
'Thwaitesii' unknown (P+ orange): *Myriotrema polytretum, M. thwaitesii.*

The chemistry of the family in Sri Lanka is rather close to that in the New World. The four commonest profiles have approximately the same frequency: no substances present (34% of the species in Sri Lanka vs 23% in Panama and Dominica), psoromic acid (21% vs 20%), stictic acid (18% vs 16%), and protocetraric acid (4% vs 8%). None of the P+ unknowns from Sri Lanka (except for the 'cinchonarum' unknown) nor salazinic acid have yet been discovered in the New World. On the other hand, one P+ unknown, the 'praestans' unknown, occurs in the New World but not in the Old (Hale 1974*a*: 36).

Ecology and conservation

As one would expect, the majority of the species in Sri Lanka occur in relatively narrow ecological niches, and for this reason information on habitat preferences can be invaluable in distinguishing the species. The commoner ones are discussed below. The less commonly collected species (e.g. those collected less than 6–8 times) unfortunately cannot be categorized with any degree of confidence and are omitted in the discussions; their habitats are briefly described in the main list of species.

Elevation has the greatest effect on the overall distribution of the Thelotremataceae. Naturally, elevation extremes are limited by the particular topography of a country and assignment of species to high or low elevation classes should be taken in a relative sense. For example, *Thelotrema weberi* occurs at the highest elevation in Sri Lanka (2520 m) but was first collected in New Guinea at 4450 m. For Sri Lanka, I define low elevation as terrain lying between sea level and about 350 m. High elevation is 2000 m and above. The few localities at about 1000 m (Enselwatta and Rassagala) have both high elevation and low elevation species although low elevation species predominate.

The high elevation species, mostly in the genus *Thelotrema*, were collected chiefly in the Nuwara Eliya district (Horton Plains), Pidurutalagala, and the Hakgala Botanical Garden. They include *Myriotrema nuwarense, Ocellularia monosporoides, Thelotrema lepadinum, T. nostalgicum, T. nureliyum, T. pidurutalagalum,* and *T. weberi.* A division of the species into base level and canopy types at this elevation is meaningless since the trees are rather low and form a broken canopy without strong vertical zonation of the epiphytes.

Low elevation species grow chiefly in virgin forests below about 350 m but sometimes occur as high as 850–1000 m. In Sri Lanka, these include *Myriotrema albocinctum, M. album, M. desquamans, M. granulosum, M. olivaceum, M. terebratulum, Ocellularia aurata, O. chonestoma, O. crassa, O. croceopora, O. dolichotata, O. keralensis, O. lankaensis, O. marivelensis, O. massalongoi, O. melanotremata, O. nylanderiana, O. papillata, O. perforata, O. polillensis, O. punctulata, O. thelotremoides, Thelotrema magnificum, T. platysporum,* and *T. scabiomarginatum.*

It is possible to classify many of the species further as being restricted to either the canopy or base level of the trunk because I was able to collect in the canopy of felled trees at logging sites. Vertical zonation of lichens is conspicuous in mature rain forests. The commonest canopy species are *Myriotrema album, M. eminens, M. microporum, M. olivaceum, M. terebratulum, Ocellularia aurata, O. exuta, Thelotrema piluliferum,* and *T. platysporum.* The preponderance of *Myriotrema* species is remarkable.

The largest group of species was restricted to the base level on exposed roots, buttresses, saplings, and the trunks up to 1–3 m in dense forest: *Myriotrema fluorescens, M. microstomum, M. thwaitesii, Ocellularia chonestoma, O. croceopora, O. dolichotata, O. lankaensis, O. massalongoi, O. melanotremata, O. papillata, O. perforata, O. thelotremoides, Thelotrema alborosellum, T. astroideum, T. colobicum, T. magnificum, T. porinoides,* and *T. scabiomarginatum.* The remaining species in the three genera are not strongly restricted to any particular level in the forest.

One of my goals in Sri Lanka was to assess the survival of the lichen flora in the face of habitat destruction first noticed by Thwaites (1864). It is most reassuring that I was able to recollect virtually all of the species which Thwaites found both in lowland rain forest and at higher elevations. One can conclude that the continuity of forest cover is still adequate to maintain a lichen population that we know to be fatally dependent on virgin rain forest.

In the last 120 years since Thwaites collected in Sri Lanka, however, there have been great and irreversible changes in the vegetation. Virtually all of the accessible forests along the west coast have been cut down for rubber plantations, general agriculture, and expansion of villages. At higher elevations (over 800 m) huge areas of rain forest were cut for tea estates even in Thwaites' time.

Only one large tract of more or less unbroken forest remains, the Sinharaja Forest Reserve, an area about 220 km² of great importance as a watershed. Even this forest is being destroyed by commercial logging, leaving behind a desolate landscape subject to erosion and at best revegetated by secondary scrub and bamboos. Logging is particularly damaging for lichens and many other organisms, since exposure to direct sunshine and desiccation can wipe them out in a matter of months after the canopy is destroyed. One can see many bleached thalli on trees still standing in logged areas. Species on felled trees that are not removed in a logging operation die off because of this changed environment, burning or overgrowth by weedy scrub.

Phytogeography

Few world lichen monographs have been based on adequate collections, and any discussions of distribution are severely limited by the poor geographic coverage. Every recent expedition by lichenologists to tropical countries has turned up totally unexpected range extensions. This is truer perhaps for the Thelotremataceae than for almost any other crustose family because they often cannot be recognized in the field without time-consuming search with a hand lens. I will try, however, to summarize very briefly the thelotreme flora and the geographic patterns that are slowly emerging for the family, basing my statements on specimens which I have personally verified.

The flora

The thelotreme flora of Sri Lanka based on collections made by Thwaites, Almquist, Alston, Wheeler and Fosberg, Moberg and Santesson comprised 36 species amongst 200 specimens (of which about 110 are Thwaites duplicates). My own excursions in 1976 and 1978 added about 715 specimens and 74 species, bringing the total of 110 species and about 915 specimens on which the present revision has been based.

Ocellularia is by far the largest genus with 41 species and 414 collections. The 10 commonest species are *O. punctulata* (46 collections), *O. chonestoma* (43), *O. papillata* (37), *O. lankaensis* (36), *O. thelotremoides* (24), *O. crassa* (18), *O. keralensis* (18), *O. nylanderiana* (17), *O. polillensis* (15), and *O. perforata* (14). Five species, *O. diacida, O. leucomelaena, O. neocavata, O. rassagala,* and *O. tenuis,* were collected only once, while the remaining 26 species were each collected between 2 and 12 times.

Myriotrema is the second most common genus, represented by 37 species and 224 collections. The commonest species, *M. olivaceum,* was collected 28 times. *Myriotrema desquamans* is represented by 23 collections, *M. rugiferum* by 23, *M. masonhalei* by 22, *M. microstomum* by 13, and *M. albocinctum* by 11. The remaining 31 species are much rarer with 1 to 9 collections apiece.

Thelotrema ranks close to *Myriotrema* with 32 species and 188 collections in Sri Lanka. The five commonest species account for 107 of these collections: *T. imperfectum* (37), *T. platysporum* (23), *T. scabiomarginatum* (18), *T. porinoides* (15), and *T. magnificum* (14). Most of the species (22) were collected 3 or fewer times, the remainder 4–11 times.

When we analyze the percentage of the flora according to genus, we find that *Thelotrema* has 29% of the species, *Myriotrema* 34%, and *Ocellularia* 37%. Panama has relatively fewer species of *Thelotrema* (21% of the flora), more *Ocellulariae* (44%), and the same number of *Myriotremata* (35%).

Phytogeographic affinities

The pantropical species in Sri Lanka may be defined very broadly as those which occur in the New World and in one or more tropical Asian countries or also in Africa, a poorly collected region, and in Australia. Using this definition, we can identify the following 34 pantropical species in Sri Lanka, about one-third of the total 110 in the flora: *Myriotrema album, M. compunctum, M. costaricense, M. glaucescens, M. glaucophaenum, M. hartii, M. minutulum, M. olivaceum, M. terebratulum, M. wightii, Ocellularia aurata, O. emersa, O. fissa, O. leucomelaena, O. lirelliformis, O. meiosperma, O. papillata, O. perforata, O. pyrenuloides, O. subsimilis, O. tenuis, O. triglyphica, Thelotrema aggregatum, T. alborosellum, T. coccineum, T. dilatatum, T. lacteum, T. lepadinum, T. leprieurii, T. monosporum, T. phlyctidioides, T. platycarpoides, T. platycarpum,* and *T. porinoides.* The species are more or less equally divided among the three genera.

A second group of 37 species occurs in Sri Lanka and in one or more Asian countries but not in the New World: *Myriotrema anamalaiense, M. andamanicum, M. cinereoglaucescens, M. desquamans, M. eminens, M. fissurinum, M. masonhalei, M. microporum, M. microstomum, M. minutum, M. polytretum, M. porinaceum, M. rugiferum, M. santessonii, M. subconforme, M. terebrans, Ocellularia chonestoma, O. crassa, O. diacida, O. dolichotata, O. eumorpha, O. keralensis, O. marivelensis, O. massalongoi, O. monosporoides, O. nylanderiana, O. orthomastia, O. polillensis, O. thelotremoides, Thelotrema colobicum, T. kamatii, T. novae-zelandiae, T. patens, T. pseudoexanthismocarpum, T. piluliferum, T. platysporum,* and *T. weberi.* The relatively large number of *Myriotrema* species and the small number of *Thelotrema* species is noteworthy when compared with the pantropical listing.

We should add to the Asian element the following 39 species which are known only from Sri Lanka. Some of these will eventually be found in the dipterocarp forests of south-east Asia: *Myriotrema albocinctum, M. decorticatum, M. elachistoteron, M. fluorescens, M. frondosum, M. granulosum, M. mastarion, M. multicavum, M. nuwarense, M. protoalbum, M. thwaitesii, Ocellularia albomaculata, O. ascidioidea, O. croceopora, O. exuta, O. kanneliyensis, O. lankaensis, O. meiospermoides, O. melanotremata, O. neocavata, O. neopertusariiformis, O. pertusariiformis, O. pluripora, O. punctulata, O. rassagala, O. rhicnopora, O. sticticans, Thelotrema astroideum, T. dissultum, T. imperfectum, T. leprocarpoides, T. magnificum, T. nostalgicum, T. nureliyum, T. pidurutalagalum, T. pulvereodiscum, T. scabiomarginatum, T. subpatens,* and *T. waasii.*

The 110 species in Sri Lanka fall into three almost equal groups, the pantropical element (34 species), the Asian element (37 species), and the endemics (39). By comparison, Panama (Hale, 1978*a*), represented by a flora of comparable size (99 species) and collecting intensity, has 28 pantropical species, 46 New World species, and 25 endemics. Of the pantropical element, Panama and Sri Lanka share only 19 species.

A further breakdown of the species in the Old World element is difficult without access to more collections. However, a number of species in Sri Lanka seem to be range extensions from the dipterocarp forests of the Philippine-Malaysian region (e.g. *Myriotrema cinereoglaucescens, M. minutum, M. polytretum, Ocellularia chonestoma, O. crassa, O. dolichotata, O. marivelensis, O. nylanderiana, O. orthomastia, O. polillensis, O. triglyphica,* and *Thelotrema patens*) and these make up the most conspicuous phytogeographic element in the flora. Considering its proximity, India has surprisingly little in common with Sri Lanka. The intensively collected Western Ghats with about 50 species and Sri Lanka with 110 share only 8 endemics: *Myriotrema anamalaiense, M. fissurinum, M. masonhalei, Ocellularia diacida, O. keralensis, O. thelotremoides, Thelotrema kamatii* and *T. pseudoexanthismocarpum.* Few if any of the 39 endemic species of Sri Lanka can be expected in India.

As I had discovered in Panama and the West Indies, the Thelotremataceae are most abundant in undisturbed, low elevation rain forest, and in Asia this is the ideal habitat for the Dipterocarpaceae. Trees in this family make up much of the forest cover below 1000 m elevation from Sri Lanka to the Philippines and Solomon Islands. We cannot say yet which of the major tropical forest biomes have the greater number of species, those in the New World or in Asia; perhaps they are equally rich. It cannot be denied, however, that the family has reached its present state of evolution and species diversity in tropical rain forests. I would not agree with Salisbury (1975: 59) that the Thelotremataceae is a temperate family which has migrated to the tropics. This may be true of *Thelotrema* but not of *Myriotrema* or *Ocellularia.*

Collecting localities

While Sri Lanka is a rather small land mass, about three-fourths the area of Austria, it embraces a very great range of land forms and vegetation types. About 10% of the island in the lower south-west portion is dense mountainous virgin rain forest. Moving to the east and north the land is flatter, quite dry, and very much disturbed. It is obvious that Sri Lanka is far from thoroughly collected and a complete study would take many years. Most collectors in the past have gone to the Nuwara Eliya-Horton Plains area, a high cool plateau not really representative of the forested area as a whole. Southwest of this plateau stretches the Sinharaja Forest Reserve, Kanneliya Forest Reserve, Gilimale Forest Reserve, and adjacent rain forest at 100–350 m elevation, little explored for lichens and now being logged selectively for Dipterocarpaceae. It is a region of high humidity, continuous heat, and abundant land leeches. This is where I concentrated my collecting efforts, taking advantage of access to the forest along freshly cut logging roads.

Unfortunately, time did not permit excursions to the 'Knuckles' east of Adam's Peak, the Badulla District, which must have an interesting, though probably less rich thelotreme flora. Nor did I visit the semi-arid scrub where several interesting species occur.

To conserve space in the species list, I have abbreviated my collecting localities as follows. All originals are in US with numerous duplicates in BM and PDA. The Thwaites collections and those by later workers are cited in full with the herbarium indicated by standard acronyms. My collection numbers in the 40 000 series were made in the trip of March 1976, those in the 50 000 series in February 1978.

1. Maliboda to Theberton Estate, Kegalla District. This is a trail near an electric transmission line at about 800 m elevation, crossing the western end of the Adam's Peak Reserve and overlooking Norton Bridge to the north. The forest is still largely virgin in the upper region.

2. Rassagala, Ratnapura District. The trail climbs to a long ridge off the Halwathura-Kanda road northwest of Balangoda at 850–900 m elevation. It is entirely virgin rain forest with mossy forest on the highest ridge. While there was no logging here, the rather low trees could be reached easily.

3a. Gilimale, Ratnapura District. This is a hilly forested region at 150–200 m elevation, the Gilimale Forest Reserve, now being logged with elephants. The canopy flora of the dipterocarp trees was sampled extensively.

3b. IBP Reserve, Ratnapura District. I sampled this virgin dipterocarp forest only briefly. It lies on a steep slope below Adam's Peak at about 200 m elevation.

4. Weddagala, Ratnapura District. This is a very large area of virgin rain forest in the Sinharaja Forest Reserve at about 300 m elevation. Mechanized logging was in operation during my first visit in 1976 but had ended by 1978. I collected from a network of logging roads over an area of perhaps 6 km^2 at 6 sites. Large samples were obtained from the canopy and from lower levels in undisturbed forest. This is the best collected area.

5. Enselwatta, Ratnapura District. This is a plateau above Deniyaya at about 1100 m elevation, a mossy forest well known to phanerogamic collectors. It is similar to Rassag but a little more exposed.

6. Hedigalla, Kalutara District. This is a virgin rain forest at about 200 m elevation east of Matugama. It is being logged actively.

7a and 7b. Morapitiya, Kalutara District. This is a continuation of the Hedigalla forest south of Badureliya. One site (7a) was called Ruhunu-Kanda, a dense rain forest at about 200 m elevation being logged now. The other site (7b) is Ambalam-pola at closer to 300 m elevation, now being logged with elephants. It includes some collections from a new roadhead about 1 km farther south. Freshly felled dipterocarp trees were available at these sites.

8. Morawaka, Matara District. This is a low mountain pass of not more than 400 m elevation near Morawaka which we traversed on an old trail. It is barely disturbed dipterocarp forest not yet logged.

9. Hiniduma, Galle District. There is an extensive area of lowland rain forest at 100–150 m elevation southeast of Hiniduma, called the Kanneliya Forest Reserve. It was being logged with machinery in 1976 and had previously been heavily logged.

10. Nuwara Eliya to Hakgala, Nuwara Eliya District. This site is a forest reserve about 1 km off the road between Nuwara Eliya and Hakgala Botanical Garden. It is a rather sheltered forest at about 2100 m elevation.

11. Hakgala Botanical Garden, Nuwara Eliya District. Thwaites collected lichens in this well known garden. The large trees are all planted. The elevation is near 2100 m.

12. Pidurutalagala, Nuwara Eliya District. This long, gently sloped mountain is the highest point in Sri Lanka (8260 ft. or 2518 m), reached by a well-worn trail. The forest along the trail has been severely disturbed since Thwaites' time. The summit is covered with a dense almost impenetrable shrub draped with *Usnea*. Most of the lichens are found on exposed branches.

13. Peradeniya Botanical Garden, Kandy District. I made a few collections on trees in this long-established garden. The elevation is about 400 m.

The richest localities were the virgin lowland rain forests. I found 44 different species in the Weddagala-Sinharaja area. There were 43 species in the Hiniduma-Kanneliya Forest Reserve and 42 in the Morapitiya area, all lying at 150–300 m elevation. By contrast only 15 species have been collected in the Nuwara Eliya region (elevation about 2000 m), one of the most frequently visited localities in Sri Lanka. There were only eight species at Pidurutalagala, the highest peak.

List of species

The 110 species of the family Thelotremataceae in Sri Lanka are listed below in alphabetic order under three genera, *Thelotrema, Myriotrema,* and *Ocellularia.* The synonymy includes species from both the New World and Old World, but I have not repeated data on synonymy previously published in my studies of the family in Dominica and Panama (Hale, 1974*a*, 1978*a*). These studies should also be consulted for additional comments on the species.

In compiling the descriptions, I have taken anatomical measurements of the cortex, algal layer, and medulla from scanning electron microscope prints and free-hand light microscope sections. Apothecial and pore size was measured from photographs reproduced at × 14 magnification. The exciple and periphysoids are best seen in sections mounted in Hoyers Solution or other clearing agents; water mounts are not satisfactory.

Chemistry is an important and useful character when studying the Thelotremataceae. While colour tests are often adequate, identification of the substances with thin-layer chromatography is desirable. Chemical constituents given in the species descriptions are those of the type material and the specimens listed.

I did not have suitable Sri Lankan material available for illustrating *Thelotrema lacteum* and *T. monosporum.* Collections from India are substituted for these. Localities for Hale collections are abbreviated 1–13 as indicated above under 'Collecting localities' (p. 247).

Key to the genera

1 Exciple with periphysoids on the inner face; columella always lacking **Thelotrema** (p. 249)
– Periphysoids lacking; columella present or absent 2
2 Exciple colourless to pale reddish brown; columnar structures, if present, noncarbonized . . . . **Myriotrema** (p. 271)
– Exciple carbonized; carbonized columella often present. . . . **Ocellularia** (p. 297)

I. THELOTREMA Ach.

Meth. Lich.: 130 (1803).

Antrocarpum G. Meyer, *Nebenstund.* : 326 (1825).
Gomphospora Trevisan in *Riv. Period. Accad. Padova* **1851-52** : 268 (1852).
Brassia Massal. in *Atti R. Ist. veneto Sci.* **III, 5** : 259 (1860).
Asteristion Leighton in *Trans. Linn. Soc. Lond.* **29** : 163 (1870).
Chroodiscus (Müll. Arg.) Müll. Arg., *Lich. Epiphyll. Novi* : 18 (1890).

Thallus crustose, epiphloeodal or hypophloeodal; cortex when present loosely organized to dense, rarely splitting and exfoliating; medulla usually rather thin or lacking; apothecia somewhat immersed to generally raised or strongly emergent, the thalline wall incurved to erect to recurved; exciple free (detached) or rarely fused (attached), the inner face covered with short periphysoids; pore often broad and gaping; spores colourless or brown, transversely septate or muriform, I+ blue or I−.

TYPE SPECIES. *Thelotrema lepadinum* (Ach.) Ach.

NUMBER OF SPECIES. About 100.

OBSERVATIONS. *Thelotrema* is amply characterized by the presence of periphysoids. There is great variability in emergence, from nearly immersed and flush (e.g. *T. kamatii*) to emergent (*T. nostalgicum*). Salisbury (1972*a*) divides *Thelotrema* sect. *Thelotrema* into two groups, the '*T. lepadinum*' group (thalline wall incurved) and the '*T. platycarpum*' group (thalline wall recurved). While extreme examples of these groups such as *T. lepadinum* (Fig. 8a) and *T. platycarpum* (Fig. 9f) are easily separated, there are a number of species with an erect thalline wall and a relatively open disc (e.g. *T. aggregatum, T. scabiomarginatum*) which are difficult to place. There is also a third small but distinctive group with emergent apothecia, a fused exciple, and psoromic acid, including *T. piluliferum* and *T. platysporum* from Sri Lanka, which do not fit in any of these categories. I feel it is premature to divide the genus into groups or formal taxa as long as so few ontogenetic studies have been made and a significant number of 'intermediates' seems to exist.

Key to the species

1 Spores colourless 2
– Spores brown 26
2 Spores transversely septate 3
– Spores muriform 17
3 Disc open, brightly pigmented purplish to orange 4
– Disc open or closed, not pigmented 6
4 Collected on evergreen leaves of trees in rain forest . . . . . **4. T. coccineum**
– Collected on tree bark 5
5 Cortex lacking; disc deep purple; spores 15–18 μm . . . . **31. T. waasii**
– Cortex present; disc orange; spores 70–90 μm . . . . . . **14. T. magnificum**
6 Spores large, 75–250 μm long, 12–30 loculate 7
– Spores small to medium sized, 10–65 μm long, 4–12 loculate 12
7 Apothecia strongly emergent and urceolate; thallus K−, P+ red (fumarprotocetraric acid) . . . . **16. T. nostalgicum**

–	Apothecia immersed to flush or semi-emergent; thallus K+ yellow, P+ orange (stictic acid) or K–, P– (no substances present)	26.	8
8	Cortex lacking; stictic acid present	26. **T. porinoides**	
–	Cortex present; no substances present		9
9	Apothecia 1–1·5 mm diam with erupting excipular material	27. **T. pseudoexanthismocarpum**	
–	Apothecia 0·4–0·8 mm diam; excipular material not erupting		10
10	Apothecia more or less emergent; thalline rim incurved to suberect; spores less than 70 μm long	8. **T. imperfectum**	
–	Apothecia immersed to flush; thalline rim barely raised; spores more than 100μm long		11
11	Spores 120–150 μm long; collected at lower elevations	9. **T. kamatii**	
–	Spores 60–120 μm long; collected at higher elevations	18. **T. nureliyum**	
12	Disc open, 1 mm wide or more; thalline rim distinctly recurved		13
–	Disc more or less closed; thalline rim low, suberect to barely recurved		15
13	Thallus corticate, dark olive green	3. **T. astroideum**	
–	Thallus lacking a cortex, whitish gray		14
14	Thallus K+ yellow, P+ orange (stictic acid)	6. **T. dilatatum**	
–	Thallus K–, P– (no substances present)	2. **T. alborosellum**	
15	Apothecia semi-emergent; thalline rim incurved; spores 35–70 μm	8. **T. imperfectum**	
–	Apothecia more or less flush; thalline rim low, becoming erect; spores 12–26 μm		16
16	Thalline rim coarse; thallus K+ yellow, P+ orange (stictic acid)	20. **T. phlyctidioides**	
–	Thalline rim delicate; thallus K–, P– (no substances)	30. **T. subpatens**	
17	Spores large, over 100 μm long		18
–	Spores smaller, less than 80 μm long		21
18	Apothecia strongly emergent, urceolate	32. **T. weberi**	
–	Apothecia flush to semi-emergent		19
19	Thallus shiny, distinctly corticate; disc filled with excipular material	29. **T. scabiomarginatum**	
–	Thallus dull, lacking a cortex; disc open		20
20	Thallus K+ yellow, P+ orange (stictic acid)	19. **T. patens**	
–	Thallus K–, P– (no substances present)	5. **T. colobicum**	
21	Pore very tiny, 0·05–0·15 mm diam; thallus P+ deep yellow (psoromic acid)		22
–	Pore gaping, 0·2–0·4 mm diam or disc open, chroodiscoid		23
22	Apothecia strongly emergent, 0·7–1·0 mm diam; pore 0·05 mm diam	22. **T. piluliferum**	
–	Apothecia raised to emergent, 0·3–0·07 mm diam; pore variable, to 0·15 mm diam	25. **T. platysporum**	
23	Thallus corticate, dark olive green	7. **T. dissultum**	
–	Thallus lacking a cortex, dull, whitish to straw coloured		24
24	Apothecia emergent; thalline rim incurved with a distinct pore	11. **T. lepadinum**	
–	Apothecia flush to barely raised; thalline rim erect to recurved, the disc open		25
25	Thallus K+ yellow, P+ orange (stictic acid)	17 **T. novae-zelandiae**	
–	Thallus K–, P– (no substances present)	13. **T. leprocarpoides**	
26	Spores transversely septate (rarely with a longitudinal septum in end cells)		27
–	Spores muriform		32
27	Spores large, 90–100μm; apothecia urceolate	21. **T. pidurutalagalum**	
–	Spores 15–60 μm long; apothecia immersed to emergent, not urceolate		28
28	Apothecia distinctly pored with an incurved thalline wall	10. **T. lacteum**	
–	Apothecian with an open disc, chroodiscoid; thalline wall erect to recurved		29
29	Thalline rim thick, pulverulent to flocculent	12. **T. leprieurii**	
–	Thalline rim thin, often recurved, entire to white pruinose		30
30	Disc 0·5–0·7 mm diam, becoming filled with excipular material; thallus K–, P– (no substances present)	1. **T. aggregatum**	
–	Disc 0·5–2·5 mm diam, open; thallus K+ yellow, P+ orange (stictic acid)		31
31	Disc 0·5–1·2 mm diam	23. **T. platycarpoides**	
–	Disc 1–2·5 mm diam	24. **T. platycarpum**	
32	Apothecia chroodiscoid; thalline rim erect, pulverulent	28. **T. pulvereodiscum**	
–	Apothecia with a distinct pore, the disc closed; thalline rim incurved	15. **T. monosporum**	

1. **Thelotrema aggregatum** (Hale) Hale in *Mycotaxon* **11** : 131 (1980).
(Fig. 7a)

Phaeotrema aggregatum Hale in *Smithson. Contr. Bot.* **16** : 29 (1974) Type: Dominica, Newfoundland, January 1969, *M. E. Hale* 35 229 (US—holotype).
Icones. Hale, 1974*a* : 26 fig. 13h (holotype).

Thallus olive greenish, 6–10 cm broad, shiny, waxy, continuous; cortex dense, 15–18 μm, with sparse aculeate hyphae, some internal splitting; algal layer continuous, 15μm; medulla 10–40 μm with crystals and periderm inclusions; apothecia more or less immersed, solitary to aggregated in dense clusters, 0·5–0·7 mm diam, the thalline rim barely discernible to emergent, suberect or even rarely weakly recurved, the tips granular and pruinose, the exciple free, apically reddish, partially filling the disc; disc dark or white pruinose; hymenium 70–90 μm; spores brown, transversely septate, 5–7 × 12–18 μm, 4–6 loculate, I+.

Chemistry. No substances present.

Habitat. Canopy branches in rain forest at lower elevations (150–300 m).

Distribution. Dominica, Sri Lanka.

Additional specimens. Hale collections: 3a (46 345), 7b (51 021). Thwaites collections: C.L. 167 (BM, PDA, S, UPS) (as 'Lgt. 84. *Thelotrema auberianum*').

Observations. This species is probably assignable to the '*Thelotrema platycarpum*' group, most closely related to *T. leprieurii* (see below), from which it can be distinguished by the smaller, aggregated apothecia. Leighton called the Thwaites material '*T. auberianum* Mont.' but this reticulate-columellate species (= *Ocellularia auberiana* (Mont.) Hale; see Hale, 1978*a* : 35) contains psoromic acid. Nylander had not verified this collection.

2. **Thelotrema alborosellum** (Nyl.) Tuck., *Gen. Lich.* : 139 (1872).
(Fig. 7b)

Graphis alborosella Nyl. in *Annls Sci. nat.* (Bot.) IV, **19** : 372 (1863). Type: Colombia, *Lindig* 2694 (H-Nyl.—lectotype; BM, FH-Tuck., UPS—isolectotypes).
Ocellularia alborosella (Nyl.) Santesson in *Symb. bot. upsal.* **12**(1) : 308 (1952).
For additional synonymy see Hale (1978*a* : 12).
Icones. Hale, 1974*a* : 18 fig. 9b (lectotype).—Hale, 1978*a* : 13 fig. 4c.

Thallus whitish, dull, to 10 cm diam; cortex lacking, the algae scattered among superficial medullary hyphae; medulla mostly hypophloeodal; apothecia chroodiscoid, to 1 mm diam, the thalline rim split and recurved, the exciple fused to barely free apically, colourless; disc tannish to whitish pruinose; hymenium 60–75 μm; spores colourless, transversely septate, 4–5 × 12–24 μm, 6–8 loculate, I−.

Chemistry. No substances present.

Habitat. Lower bole in rain forest or disturbed sites at 200–2100 m elevation.

Distribution. United States, West Indies, Central and South America, India, Sri Lanka.

Additional specimens. Hale collections: 1 (50209), 2 (51 122, 51 236), 4 (50 426), 10 (50 269).

Observations. This species is quite variable (see discussions under *Ocellularia alborosella* in Hale, 1974*a* : 16 and 1978*a* : 12) and my identifications encompass a rather broad population. The type specimen (and material from Sri Lanka) definitely lacks a cortex. Nylander gives spore size as 5–6 × 20–23 μm and my collections from Sri Lanka fall in this range.

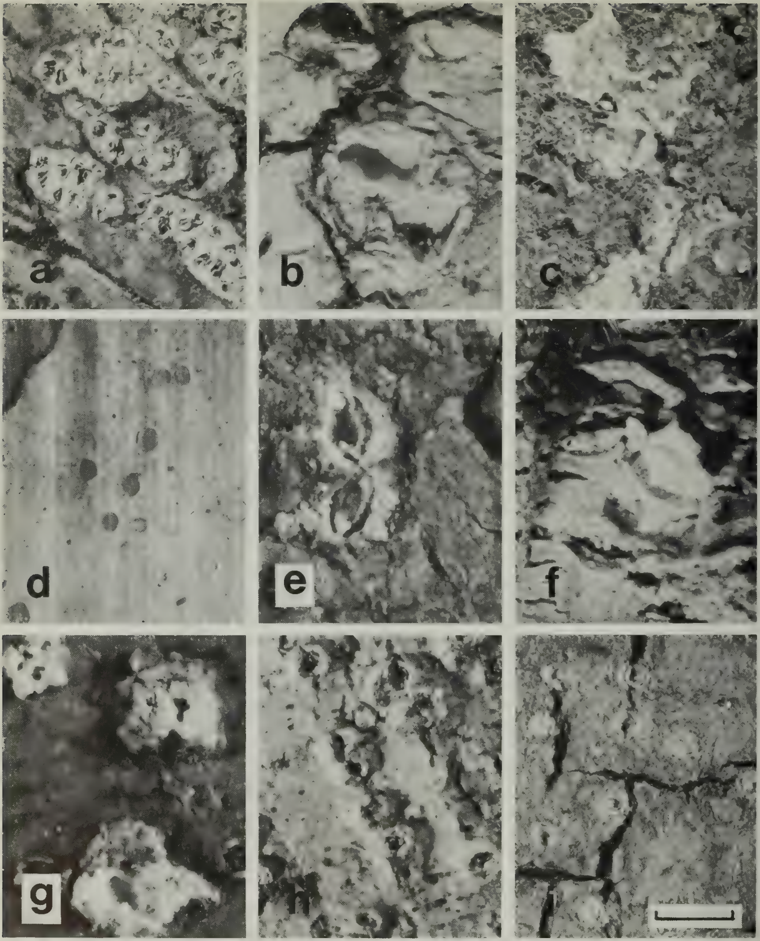

Fig. 7 Species of *Thelotrema*. (a) *T. aggregatum* (Hale, 51 021). (b) *T. alborosellum* (Hale 50 269). (c) *T. astroideum* (Hale 47 035). (d) *T. coccineum* (Thwaites s.n. in BM). (e) *T. colobicum* (Hale 50 251). (f) *T. dilatatum* (Hale 46 218). (g) *T. dissultum* (Hale 51 139). (h) *T. imperfectum* (Hale 50 433). (i) *T. kamatii* (Hale 50 098). Scale in Fig. 7i = 1 mm.

3. Thelotrema astroideum (Berk. & Broome) Hale in *Mycotaxon* **11** : 131 (1980).
(Fig. 7c)

Platygrapha astroidea Berk. & Broome in *J. Linn. Soc.* (Bot.) **14** : 109 (1875). Type: Sri Lanka, *Thwaites* 629 (K—lectotype).
Ocellularia astroidea (Berk. & Broome) Hale in *Mycotaxon* **7** : 377 (1978).
ICONES. Hale 1978*b* : 384 fig. 1.

Thallus dark greenish or brownish gray, 6–15 cm broad, shiny, continuous; cortex dense, 10–20 μm; algal layer 10–15 μm; medulla not distinct, mostly hypophloeodal; apothecia chroodiscoid, 0·8–1·2 mm diam, the thalline rim split and recurved, the exciple fused with short periphysoids; disc and inner surface of thalline wall white pruinose; hymenium 40–65 μm; spores colourless, transversely septate, 3–5 × 10–18 μm, 4–6 loculate, I−.

CHEMISTRY. No substances present.

HABITAT. Base and lower bole, saplings in rain forest at low to mid elevations (150–900 m).

DISTRIBUTION. Sri Lanka.

ADDITIONAL SPECIMENS. Hale collections: 2 (51 157, 51 177, 51 199, 51 203), 3 a (46 297, 46 365), 4 (47 127), 7a (50 164), 7b (51 103), 8(47 037).

OBSERVATIONS. The contrast between the dark waxy greenish thallus and the large white apothecia make this a conspicuous species. It can be differentiated from *T. alborosellum* by the presence of a cortex as well as by the more delicate, strongly recurved thalline margin. It is known only from Sri Lanka (Hale, 1978*b* : 377).

4. Thelotrema coccineum (Leighton) Hale in *Mycotaxon* **11** : 131 (1980).
(Fig. 7d)

Platygrapha coccinea Leighton in *Trans. Linn. Soc. Lond.* **25** : 456 (1866). Type: Brazil, *Spruce* (not seen).
Ocellularia coccinea (Leighton) Müll. Arg. in *Flora, Jena* **66** : 353 (1883).
Chroodiscus coccineus (Leighton) Müll. Arg., *Lich. Epiphyll. Novi* : 18 (1890).
See Santesson (1952 : 309) for full synonymy.

Thallus foliicolous, greenish, 2 cm broad; cortex lacking; apothecia chroodiscoid, barely erumpent, 0·2–0·4 mm diam, the thalline rim recurved, exciple free; disc plane, scarlet; hymenium 35–60 μm; spores colourless, transversely septate, 2–4 × 8–12 μm, 2–4 loculate (spore data from Santesson).

CHEMISTRY. K+ purple epithecial pigment.

HABITAT. Palm leaves.

DISTRIBUTION. Pantropical.

SPECIMEN. Sri Lanka, *Thwaites* s.n. (BM).

OBSERVATIONS. Santesson recognized this epiphyllous species as *Chroodiscus coccineus* (Leighton) Müll. Arg. with some hesitation since the thin-walled spores are not basically different from those in other chroodiscoid species. I am listing it under *Thelotrema*.

5. Thelotrema colobicum Nyl. in *Bull. Soc. Linn. Normandie* II, 7 : 169 (1873).
(Fig. 7e)

Type: India, Andaman Islands, 1867, *Kurz* (H-Nyl. 22493—lectotype).
Thelotrema deightonii C. Dodge, *Beih. nov. Hedwigia* **12** : 100 (1964). Type: Sierra Leone, Kori, Njala, *Deighton* M5856 (BM—holotype).

Thallus whitish gray, 4–12 cm broad, dull, continuous; cortex very thin as a polysaccharide layer with aculeate hyphae or lacking; algal layer dispersed among superficial medullary hyphae; medulla mostly hypophloeodal; apothecia sparse, chroodiscoid, 0·9–1·2 mm diam, the thalline rim suberect to recurved, split, exciple free, partially filling the disc; disc white pruinose; hymenium *c.* 130 μm; spores colourless, muriform, 28–30 × 130–150 μm, with numerous cells, I–.

CHEMISTRY. No substances present.

HABITAT. Lower trunks of trees in mossy forest at mid elevations (850–1100 m).

DISTRIBUTION. Sierra Leone, India, Sri Lanka.

ADDITIONAL SPECIMENS. Hale collections : 1 (50 198), 5 (46 222, 46 234, 46 251).

OBSERVATIONS. This member of the '*Thelotrema platycarpum*' group has large spores. It is probably close to *T. leprocarpum* Tuck., a New World species, which has somewhat smaller spores (less than 100 μm) and smaller apothecia. Nylander compared it with *T. leucophthalmum* Nyl., which contains stictic acid, is definitely corticate, and has small spores (23–35 μm long).

6. Thelotrema dilatatum (Müll. Arg.) Hale in *Mycotaxon* **11** : 131 (1980).
(Fig. 7h)

Ocellularia dilatata Müll Arg. in *J. Linn. Soc.* (Bot.) **30** : 452 (1895). Type: Brazil, Rio de Janeiro, *Glaziou* 5531 pp. (G—lectotype; BM—isolectotype).
ICONES. Hale, 1974*a* : 21 fig. 11a (lectotype) and fig. 11b—Hale, 1978*a* : 18 fig. 5h.

Thallus whitish ashy, about 2 cm broad; cortex lacking; algae scattered among patches of medullary hyphae; medulla mostly hypophloeodal; apothecia rather rare, chroodiscoid, about 1 mm diam, the thalline rim coarse, split and recurved, the inner surface and disc densely white pruinose, the exciple fused; disc open, white pruinose; hymenium 130 μm; spores colourless, transversely septate, 6–8 × 30 μm, 5–7 loculate, I+.

CHEMISTRY. Stictic and constictic acids.

HABITAT. Canopy branch in rain forest at low elevations (150 m).

DISTRIBUTION. West Indies, Central and South America, Sri Lanka.

ADDITIONAL SPECIMENS. Hale collections: 9 (46 218).

OBSERVATIONS. This species was previously known only from the New World. It is characterized by the lack of a cortex and large, often irregularly elongate apothecia with a thick thalline rim. Similar species in Sri Lanka include *T. magnificum* and *T. waasii*, which have pigmented discs, and *T. patens.*

7. Thelotrema dissultum Hale **sp. nov.**
(Fig. 7g)

Thallus corticola, epiphloeodes, obscure viridis, 4–8 cm latus; apothecia conspicua, chroodiscoidea, thallum superantia, 1–1·5 mm diametro, margine thallino erecto vel recurvato, late fisso, subgranulato, excipulo crasso, periphysoidibus instructis, disco albo pruinoso; hymenium 70–90 μm altum; sporae incolores, murales, octonae, 5–8 × 14–16 μm, 1–2 × 6–7 loculatae, I–.

Typus: Sri Lanka, Sabaragamuwa Province, Ratnapura District, Halwathura-Kanda, near Rassagala, elev. 900 m, 15 Mar. 1978, *M. E. Hale* 51 139 (US—holotypus; BM—isotypus).

Thallus dark greenish gray, 4–8 cm broad, shiny, continuous; cortex dense, 15–18 μm; algal layer continuous, 15–25 μm; medulla to 150 μm with periderm and crystalline inclusions; apothecia conspicuous, 1–1·5 mm diam, the thalline rim erect to barely recurved, thick, coarsely split and subgranular at maturity, white, the exciple free, coarse; disc partially closed, white pruinose; hymenium 79–90 μm; spores colourless, muriform, 5–8 × 14–16 μm, 1–2 × 6–7 loculatae, I–.

CHEMISTRY. Stictic acid.

HABITAT. Trees along trails in mossy forest at mid elevations (900 m).

DISTRIBUTION. Sri Lanka.

ADDITIONAL SPECIMENS. Hale collections: 2 (51 213, 51 235).

OBSERVATIONS. The dark waxy thallus provides a sharp backdrop for the large, white erupting apothecia. The thalline wall is generally erect with some tendency to recurve. There are no close relatives in the genus.

8. **Thelotrema imperfectum** Hale **sp. nov.**

(Fig. 7h)

Thallus corticola, epiphloeodes, tenuis, nitidus, pallide brunneus, 8–14 cm latus; apothecia dispersa, inconspicua, semi-emergentia vel immersa, 0·5–0·8 mm diametro, margine thallino integro vel minute lacerato, decolorato, excipulo distincto, libero, periphysoidibus instructis; ostiolum rotundatum, 0·2–0·4 mm diametro; hymenium 110–180 μm altum; sporae incolores, transversim septatae, 4–8 : nae, 6–12 × 35–70 μm, 12–18 loculatae, I+ coeruleae.

Typus: Sri Lanka, Sabaragamuwa Province, Ratnapura District, Sinharaja Forest Reserve near Weddagala, elev. 300 m, 14 Mar. 1978, *M. E. Hale* 50 443 (US—holotypus; BM—isotypus).

Thallus greenish to olive whitish gray, 8–14 cm broad, thin, continuous; cortex loosely organized, 15–20 μm; algal layer 10 μm; medulla about 15 μm with numerous crystals; apothecia numerous, nearly flush to semi-emergent, 0·5–0·8 mm diam, the thalline rim ragged, crumbling apically, suberect, exciple apically free, rather coarse and filling the disc, in part as an inner pore, periphysoids present; pore gaping, 0·2–0·4 mm diam; hymenium 110–180 μm; spores colourless, transversely septate, 6–12 × 35–70 μm, 4–8/ascus, 12–18 loculate, I+.

CHEMISTRY. No substances present.

HABITAT. Tree base, lower trunk, and saplings in rain forest at low to mid or higher elevations (150–2000 m).

DISTRIBUTION. Sri Lanka.

ADDITIONAL SPECIMENS. Hale collections: 1 (50, 193, 50 199, 50 229), 2 (51 172, 51 218, 51 221), 3a (46 346, 46 362), 4 (47 067, 47 110, 47 125, 47 128, 47 136, 50 378, 50 385, 50 394, 50 400, 50 409, 50 410, 50 420, 50 422, 50 434, 50 441, 50 489, 50 491, 50 495, 50 518), 5 (46 233, 46 239, 46 272, 46 276), 7b (50 295, 51 031, 51 085), 9 (46 155), 10 (50 281).

OBSERVATIONS. It is remarkable that a species as common as this was not collected by Thwaites. At first it seemed to be an anomalous population of *T. subtile* Tuck. but the spores are significantly, and consistently, larger (*T. subtile* has spores 25–35 μm long), the pore is ragged and coarsely pruinose, and the apothecia are in general somewhat raised. Another species here, *T. kamatii* (see below), has even larger spores, 120–150 μm long, more or less flush apothecia, and an entire, barely raised rim, and a fourth one, *T. nureliyum* (below), occurring at higher elevations, has large spores and a coarser exciple. All of these species are related by the presence of periphysoids and lack of chemistry.

9. **Thelotrema kamatii** (Patw. & C. Kulk.) Hale in *Mycotaxon* **11** : 131 (1980).

(Fig. 7i)

Ocellularia kamatii Patw. & C. Kulk. in *Norw. J. Bot.* **24** : 130 (1977). Type: India, Karnataka, Carmudi Ghat, *M. B. Nagarkar & K. D. Gole* 76·1061 (AMH—holotype; US—isotype).

ICONES. Patwardhan & Kulkarni, 1977 : 129 fig. 6.

Thallus pale olive greenish, 6–10 cm broad, thin, dull; cortex dense, variable, 10–20 μm; algal layer 10–15 μm, discontinuous among subcortical crystals; medulla 30–90 μm with dense crystals; apothecia numerous, round, 0·3–0·4 mm diam, more or less flush to slightly raised, the thalline rim entire to crenate, exciple free, more or less filling the pore at maturity; pore gaping, *c.* 0·3 mm diam; hymenium 180–200 μm; spores colourless, transversely septate, 10–25 × 120–150 μm, 16–22 loculate, 2–4/ascus, I+.

CHEMISTRY. No substances present.

HABITAT. Canopy branches in rain forest at low elevations (300 m).

DISTRIBUTION. India, Sri Lanka.

ADDITIONAL SPECIMENS. Hale collections: 7a (50 098, 50 166).

OBSERVATIONS. The relation of this species to *T. imperfectum, T. nureliyum,* and *T. subtile* is discussed above under *T. imperfectum*. The spores of the type collection do react I+ blue, although the original description says iodine negative (Patwardhan & Kulkarni, 1977). This is one of the few species collected so far only in India and Sri Lanka.

10. **Thelotrema lacteum** Krempelh. in Nyl. in *Flora, Jena* **47** : 269 (1864). (Fig. 8a)

Type: Australia, comm. Hochstetter (M—lectotype).

Thelotrema cavatum var. *dolichosporum* Nyl. in *Annls Sci. nat.* (Bot.) IV, **11** : 242 (1859). Type: Polynesia, Marquesas, Nuku Hiva, *Mercier* s.n. (PC—lectotype).

Thelotrema dolichosporum (Nyl.) Nyl. in *Bull Soc. linn. Normandie* II, **2** : 72 (1868).

Ocellularia dolichospora (Nyl.) Müll Arg. in *Mem. Soc. Phys. Hist. nat. Genève* **29**(8) : **9** (1887).

Phaeotrema lacteum (Krempelh. in Nyl.) Müll. Arg. in *Flora, Jena* **70** : 398 (1887).

Ocellularia cricota F. Wilson in Bailey in *Queensl. Dept. Agric. Bull.* **7** : 32 (1891). Type: Australia, Southport, *Wilson* s.n. (G—lectotype).

Phaeotrema cricotum (F. Wilson) Müll. Arg. in *Hedwigia* **32** :130 (1893).

Ocellularia japonica Zahlbr. in *Annls Mycol.* **14** : 49 (1916). Type: Japan, Prov. Kotsuke, Mt Akagi, *Tsunoda* s.n. (W—lectotype).

For additional synonymy see Salisbury, 1972*a* : 270 (as *Thelotrema lepadodes*) and Hale, 1974*a* : 29 (as *Phaeotrema disciforme*).

ICONES. Salisbury, 1971*b* : 272 fig. 1 (as *Thelotrema lepadodes*) and 1972*a* : 270 fig. 8 (as *Thelotrema lepadodes*).—Hale, 1974*a* : 30 fig. 14a (as *Phaeotrema disciforme*).

Thallus straw coloured, 6–8 cm broad, thin, shiny, rugulose; cortex lacking; algae scattered among superficial medullary hyphae; medulla mostly hypophloeodal; apothecia emergent, 0·7–1·0 mm diam, the exciple free, colourless, pulling away from the wall with the disc; pore gaping, 0·2–0·4 mm diam; hymenium 90–110 μm; spores brown, transversely septate, 6–10 × 33–60 μm, 7–11 loculate, I−.

CHEMISTRY. No substances present.

HABITAT. Lower trunks of trees in rain forest at lower elevations (150–300 m).

DISTRIBUTION. United States, West Indies, Central America, Kenya, Mozambique, South Africa, Assam, India, Sri Lanka, Japan, New Guinea, Australia, Solomon Islands, New Caledonia, Polynesia, Hawaii.

ADDITIONAL SPECIMENS. Hale collections: 7a (50 161), 9 (46 268). Thwaites collections: C. L. 128 (BM, PDA) (as 'Lgt. 93. *Thelotrema disciforme*') (other duplicates in BM and those in S, UPS are *Thelotrema monosporum*).

OBSERVATIONS. As one may deduce from the extensive synonymy, this pantropical species has not been well understood. It is more or less identical with *T. monosporum* (below) except for the transversely septate spores. They often occur together in low elevation secondary forests. The spores of *T. lacteum* appear to be smaller, often not more than 65 μm, than those

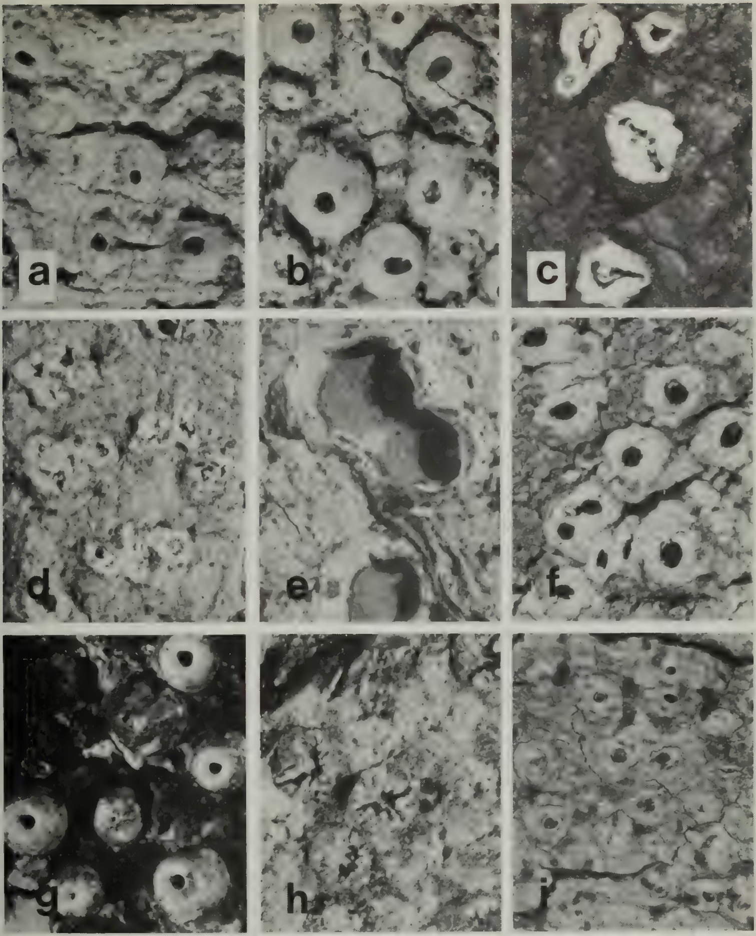

Fig. 8 Species of *Thelotrema*. (a) *T. lacteum* (Patwardhan 74·2102 in US). (b) *T. lepadinum* (Hale 50 357). (c) *T. leprieurii* (Hale 46 123). (d) *T. leprocarpoides* (Hale 50 294). (e) *T. magnificum* (Hale 46 284). (f) *T. monosporum* (Patwardhan 73·1477 in US). (g) *T. nostalgicum* (Hale 50 343). (h) *T. novae-zelandiae* (Hale 50 261). (i) *T. nureliyum* (Hale 50 292). See Fig. 7i for scale.

of *T. monosporum* (120–210 μm long), but this character needs more study. Salisbury (1972*a* : 270) lists *Phaeotrema rockii* Zahlbr. (= *Thelotrema rockii* (Zahlbr.) Hale) as a synonym but I would prefer to recognize it as a distinct species because it contains stictic acid.

11. Thelotrema lepadinum (Ach.) Ach., *Meth. Lich.:* 132 (1803).
(Fig. 8b)

Lichen lepadinus Ach., *Lich. Suec. Prodr.:* 30 (1798). Type: Sweden, *Acharius* s.n. (H-Ach.—lectotype; BM, UPS—isolectotypes).
*Thelotrema lepadinum *lepadizum* Nyl. in *Acta Soc. Scient. fenn.* **26** : 17 (1900). Type: Sri Lanka, Peradeniya, *Almquist* s.n. (H-Nyl.—lectotype; S—isolectotype).
For additional synonymy see Salisbury (1972*a* :267).
Icones. Redinger, 1936 : 82 fig. 47.—Salisbury, 1972*a* : 268 fig. 5.—Hale, 1978*a* : 40 fig. 12k.

Thallus whitish to pale tan, 2–6 cm broad, dull, continuous; cortex lacking; algal layer scattered among superficial hyphae; medulla mostly hypophloeodal; apothecia emergent, 0·6–1·2 mm diam, the thalline rim suberect, the exciple free, colourless, partially filling the disc; pore gaping, round, 0·2–0·4 mm diam; hymenium 120–190 μm; spores colourless, muriform, 15–20 × 65–80 μm, 1–2 × 12–14 loculate, 2–4/ascus, I–.

Chemistry. No substances present.

Habitat. Lower trunk and branches of trees at higher elevations (1500–2200 m).

Distribution. Canada, United States, Central and South America, Europe, Africa, India, Sri Lanka, Japan, Australia, New Zealand, Hawaii.

Additional specimens. Hale collections: 12 (50 357). Other collections: Nuwara Eliya District, *Santesson* 26 012 (S, US), *Moberg* 2537 (UPS).

Observations. This pantemperate weed is not nearly as common in Sri Lanka as it is in the nearby mountains of southern India.

12. Thelotrema leprieurii (Mont.) Hale in *Mycotaxon* **11** : 131 (1980).
(Fig. 8c)

Stictis leprieurii Mont. in *Annls Sci. nat.* (Bot.) IV, **3** : 97 (1855). Type: French Guiana, *Leprieur* 804 (PC—lectotype; G—isolectotype).
Graphis subnivescens Nyl. in *Flora, Jena* **69** : 174 (1886). Type: 'Insulae Guineenses', São Tomé, *Moller* s.n. (H-Nyl. 7507—lectotype).
Graphis phlyctidea Vainio in *Suomal. Tiedeakat. Toim.* A. **15**(6) : 237 (1921). Type: Philippines, Luzon, Sorsogon, Irosin, *Elmer* 14 646 (TUR—lectotype)..
Phaeographis phlyctidea (Vainio) Zahlbr., *Cat. Lich. Univers.* **2** : 383 (1923).
Phaeographis subnivescens (Nyl.) Zahlbr., *Cat. Lich. Univers.* **2** : 387 (1923).
Phaeotrema leprieurii (Mont.) Sherwood in *Mycotaxon* **5** : 203 (1977).
For additional synonymy see Salisbury, 1972*b* : 288 (as *Thelotrema leucastrum*).
Icones. Salisbury, 1972*b* : 287 fig. 9 (as *Thelotrema leucastrum*).

Thallus dark olive green, 5–8 cm broad, shiny, continuous; cortex poorly developed to lacking; algal layer 10–15 μm, scattered in the upper medullary layer between crystals; medulla 10–30 μm, with numerous periderm and crystalline inclusions; apothecia dispersed, chroodiscoid, round to irregularly elongate, 1–2 mm wide, the thalline rim suberect, inner wall and tips coarsely white-pruinose, the exciple free at the tips; hymenium 90–110 μm; spores brown, transversely septate, 5–10 × 12–18 μm, 4–5 loculate, I—.

Chemistry. No substances present.

Habitat. Open base of trees to canopy in rain forest at lower elevations (150–350 m).

Distribution. West Indies, South America, west Africa, India, Sri Lanka, Sumatra, Philippines.

ADDITIONAL SPECIMENS. Hale collections: 4 (50 397), 7a (50 155), 9 (46 123).

OBSERVATIONS. The main feature of this species is the conspicuous, sometimes flocculant exciple, although this varies and is not highly developed in the Sri Lankan material. When Vainio described *Thelotrema confluens*, he actually compared it with Nylander's *Graphis subnivescens*.

13. Thelotrema leprocarpoides Hale sp. nov.

(Fig. 8d)

Thallus corticola, hypophloeodes, opacus, albo-cinereus, 8–12 cm latus; apothecia rotundata vel pauce elongata, 0·4–0·6 mm diametro, margine thallino vix elevato vel suberecto, excipulo libero, crasso, periphysoidibus instructis, disco aperto; hymenium 90 μm altum; sporae incolores, murales, 4–8 : nae, 10–12 × 36–40 μm, 1–3 × 8–10 loculatae, I–.

Typus: Sri Lanka, Sabaragamuwa Province, Ratnapura District, near Pagoda south of Ratnapura, 12 Feb. 1976, *M. E. Hale* 46 381 (US—holotypus; BM—isotypus).

Thallus whitish mineral gray, 8–12 cm broad, thin, dull, continuous; cortex not developed; algal layer distinct, 10–15 μm, interrupted by crystals; medullary area in part epiphloeodal, 10–90 μm, consisting mostly of oxalate crystals; apothecia round to somewhat elongate, 0·4–0·6 mm diam, solitary or aggregated in twos and threes, the thalline rim barely developed, low to suberect and splitting, barely recurved, the exciple free, coarse, partially filling the disc; hymenium 90 μm; spores colourless, muriform, 10–12 × 36–40μm, 1–3 × 8–10 loculate, 4–8/ascus, I–.

CHEMISTRY. No substances present.

HABITAT. Cultivated trees at lower elevations (150–200 m).

DISTRIBUTION. India, Sri Lanka.

ADDITIONAL SPECIMENS. Hale collections: 9 (Rest House at Hiniduma, 46 380). India: Karnataka, Koppa-Sringeri road, *Hale* 49 949 (US).

OBSERVATIONS. This represents another addition to the '*Thelotrema platycarpum*' group. It is distinguished by the pruinose disc and exciple as well as lack of any chemistry.

14. Thelotrema magnificum (Berk. & Broome) Hale in *Mycotaxon* 11 : 131 (1980).

(Fig. 8e)

Platygrapha magnifica Berk. & Broome in *J. Linn. Soc.* (Bot.) **14** : 110 (1875). Type: Sri Lanka, *Thwaites* 624 (K—lectotype).
Ocellularia magnifica (Berk. & Broome) Sherwood in *Mycotaxon* 3(2) : 234 (1976).
ICONES. Sherwood, 1976 : 237 fig. 2.

Thallus greenish mineral gray, 10–15 cm broad, smooth, continuous; cortex dense, 15–20 μm, with aculeate hyphae, splitting somewhat internally; algal layer continuous, 15–20 μm; medulla 6–15 μm, mostly hypophloeodal; apothecia very conspicuous, chroodiscoid, 1–2 mm diam, the thalline rim coarse, strongly emergent and erect to recurved, the exciple fused; disc open, broad, flat, orange-red pruinose; hymenium 150–180 μm; spores colourless, transversely septate, 8–10 × 70–90 μm, 18–22 loculate, 4–6/ascus, I+.

CHEMISTRY. No medullary substances present; epithelial pigment K+ deep purple.

HABITAT. Base and lower trunk of trees in rain forest at lower elevations (150–550 m).

DISTRIBUTION. Sri Lanka.

ADDITIONAL SPECIMENS. Hale collections: 1 (50 217), 2 (51 111, 51 156), 3a (46 284, 46 348), 4 (47 090, 47 112, 50 456, 50 481), 7b (50 296, 51 034), 9 (46 149, 46 168).

OBSERVATIONS. This conspicuous lichen was described as a fungus and therefore escaped the attention of both Leighton and Zahlbruckner. Sherwood was the first to determine its correct status during a revision of the fungal genus *Platygrapha*. Berkeley and Broome had labelled the type 'Platygrapha lateritia' but changed the name before publication. It is still known only from Sri Lanka where it is common, more than my 13 collections suggest, since I could recognize it in the field by the brilliant orange-red discs and therefore only representative specimens were collected.

15. Thelotrema monosporum Nyl. in *Annls Sci. nat.* (Bot.) IV, **15** : 46 (1860). (Fig. 8f)

Type: New Caledonia, *Pancher* s.n. (H-Nyl. 22709—lectotype).
Thelotrema disciforme Leighton in *Tran. Linn. Soc. Lond.* **27** : 170 (1870). Type: Sri Lanka, *Thwaites* C.L. 128 (BM—lectotype; G, H-Nyl. 3851, PC, PDA, S, UPS, W—isolectotypes (as 'Lgt. 93. *Thelotrema disciforme*').
Leptotrema monosporum (Nyl.) Müll. Arg. in *Bull. Soc. r. Bot. Belg.* **31** : 35 (1892).
For additional synonymy see Salisbury (1972*a* : 271) and Hale (1978*a* : 52) (as *L. lepadodes*).
ICONES. Salisbury, 1972*a* : 272 fig. 10; Hale, 1978*a* : 51 fig. 14f (as *L. lepadodes*).

Thallus tannish gray, 2–4 cm broad, dull, continuous; cortex lacking; algae scattered among superficial medullary hyphae; medulla mostly hypophloeodal; apothecia emergent, 0·7–1·1 mm diam, the exciple free, pulling away from the thalline wall with the disc; hymenium 100–140 μm; spores brown, muriform, 7–12 × 45–60 μm, 1–3 × 22–24 loculate, 2–4/ascus, I−.

CHEMISTRY. No substances present.

HABITAT. Typically found in secondary forests. I did not recollect it in Sri Lanka but it can be expected to occur in the drier areas of the island.

DISTRIBUTION. Pantropical.

OBSERVATIONS. This species forms part of a complex with emergent apothecia, a periphysoid-bearing exciple, and a non-corticate thallus, including at the world level, *T. lepadinum, T. hawaiiense* (Hale) Hale, *T. lacteum,* and *T. rockii* (Zahlbr.) Hale. To these we might add closely related *T. conferendum* Hale (Hale, 1975 : 176) and *T. porinoides* (below), both of which have less emergent, nearly flush apothecia. I am adopting Salisbury's (1975 : 59) interpretation of the type of *Thelotrema monosporum* for the sake of stabilizing the nomenclature instead of using *T. lepadodes*, although I feel that the Helsinki material (there is none in PC) is so fragmentary that the only certain character is the presence of brown spores.

16. Thelotrema nostalgicum G. Salisbury in *Lichenologist* **5** : 266 (1972). (Fig. 8g)

Type: Sri Lanka, Pidurutalagala, 1879, *Almquist* s.n. (H-Nyl. 22 741—lectotype; S—isolectotype).
ICONES. Salisbury, 1972*a* : 266 fig. 3.

Thallus whitish mineral gray, 3–5 cm diam, shiny, verruculose; cortex probably lacking; algal layer scattered among superficial medullary hyphae, to 15 μm; medulla largely hypophloeodal; apothecia conspicuous, strongly emergent and urceolate, 1 mm high, 0·7–1·2 mm diam, the amphithecium smooth, corticated, exciple apically free, barely visible around the disc at base of apothecial cavity; pore round, 0·1–0·3 mm diam; hymenium 180–240 μm; spores colourless, transversely septate, 25–33 × 180–200 μm, 25–30 loculate, 1–4/ascus, I+.

CHEMISTRY. Fumarprotocetraric acid and traces of protocetraric acid.

HABITAT. Twigs of exposed shrubs at high elevations (2400 m).

DISTRIBUTION. Sri Lanka.

ADDITIONAL SPECIMENS. Hale collections: 12 (50 343, 50 356).

OBSERVATIONS. Salisbury described his new species from a fragment collected by Almquist. I was able to revisit the type locality and make additional collections. Externally it is close to *T. pidurutalagalum* and *T. weberi* (see below), two other high elevation species in the Nuwara Eliya region with urceolate, periphysoid-bearing apothecia. *Thelotrema nostalgicum* is distinguished by the unusual chemistry.

17. **Thelotrema novae-zelandiae** Szat. in *Borbásia* **1** : 56 (1939).
(Fig. 8h)

Type: New Zealand, Waikare-Moana, 1932, *J. Jablonzky* s.n. (BP—lectotype).

Thallus tannish gray, 2–3 cm diam, dull, continuous; cortex not clearly developed; algal layer scattered in superficial medullary hyphae 10–20 μm thick; medulla mostly hypophloeodal; apothecia chroodiscoid, 0·7–0·9 mm diam, the thalline rim split, incurved at first, later becoming recurved, arching over the disc, the exciple free; hymenium 130–140 μm; spores colourless, muriform, 12–15 × 50–60 μm, with numerous cells, 1–2/ascus, I−.

CHEMISTRY. Stictic and constictic acids.

HABITAT. Base of trees in open forest at higher elevations (2100 m).

DISTRIBUTION. Sri Lanka, New Zealand.

ADDITIONAL SPECIMENS. Hale collections: 10 (50 261).

OBSERVATIONS. This is the first report of the species since it was published. The Sri Lankan material has somewhat smaller apothecia than the type but the same chemistry and incurved, *Geaster*-like rim to the apothecia.

18. **Thelotrema nureliyum** Hale **sp. nov.**
(Fig. 8i)

Thallus corticola, ephiphloeodes, pallide stramineo-cinerascens, 3–5 cm latus; apothecia immersa vel semi-emergentia, 0·4–0·6 mm diam, margine thallino erecto, excipulo libero, periphysoidibus instructis; hymenium 150–160 μm altum; sporae incolores, tranversim septatae, 7–15 × 60–120 μm, 4 : nae, 22–24 loculatae, I+ coeruleae.

Typus: Sri Lanka, Central Province, Nuwara Eliya District, between Nuwara Eliya and Hakgala, elev. 2100 m, 21 Mar. 1978, *M. E. Hale* 50 292 (US—holotypus).

Thallus pale yellowish or whitish gray, 3–5 cm broad, appearing rather thick, dull, fissured; cortex weakly organized, irregularly pored, 10–15 μm; algal layer 10–12 μm; medulla 10 μm or more but largely hypophloeodal, with large crystals; apothecia numerous, partially immersed in the periderm, 0·4–0·6 mm diam, the thalline rim raised but not erect, exciple free, coarse, sometimes partially filling the pore, periphysoids present; pore round, 0·1–0·2 mm diam, the disc visible inside; hymenium 150–160 μm; spores colourless, transversely septate, 7–15 × 60–120 μm, 20–24 loculate, 4/ascus, I+.

CHEMISTRY. No substances present.

HABITAT. Tree branches in rain forest at high elevations (850–2100 m).

DISTRIBUTION. Sri Lanka.

ADDITIONAL SPECIMENS. Hale collections: 2 (51 208), 10 (50 268).

OBSERVATIONS. *Thelotrema nureliyum* is a member of the *T. subtile* complex, a difficult group of species with periphysoids but no lichen substances. It has large spores, in the range of *T. kamatii* (see above), which has a thicker, pruinose exciple and rather sparse apothecia. The few collections available indicate a high elevation habitat for *T. nureliyum* in contrast to that of *T. imperfectum*, a similar but smaller spored species which grows at lower elevations.

19. Thelotrema patens Nyl. in *Acta Soc. Scient. fenn.* **26** : 17 (1900).
(Fig. 9a)

Type: Sri Lanka, Pidurutalagala, Dec. 1879, *Almquist* s.n. (H-Nyl. 22551—lectotype; S—isolectotype).

Thallus tannish white, 2–6 cm broad, dull, smooth and continuous; cortex lacking; algal layer more or less continuous among superficial hyphae, to 15 μm; medulla mostly hypophloeodal; apothecia dispersed, solitary, chroodiscoid, 1–2 mm diam, the thalline rim split and recurved, the inner surface pruinose and subgranular, the exciple fused; disc plane, brownish to white pruinose; hymenium 110–180 μm; spores colourless, muriform, 18–25 × 80–125 μm, with numerous cells, 1–4/ascus, I−.

CHEMISTRY. Stictic and constictic acids.

HABITAT. On trunks and branches of trees in rain forest at lower mid to high elevations (300–2200 m).

DISTRIBUTION. Sri Lanka, Sarawak.

ADDITIONAL SPECIMENS. Hale collections: 1 (50 254), 7b (50 312).

OBSERVATIONS. I did not recollect this species on Pidurutalagala but found it in lower elevation rain forest. It externally resembles *T. dilatatum*, which has smaller, I+ blue spores.

20. Thelotrema phlyctidiodes (Müll. Arg.) Hale in *Mycotaxon* **11** : 132 (1980).
(Fig. 9b)

Ocellularia phlyctidioides Müll Arg. in *Hedwigia* **32** : 130 (1893). Type: Australia, Brisbane, *Bailey* 354 (G—lectotype).

Ocellularia conglomerata Hale in *Smithson. Contr. Bot.* **16** : 19 (1974). Type: Dominica, *Hale* 37 959 (US—holotype).

ICONES. Hale, 1974*a* : 18 fig. 9h.—Hale 1978*a* : 18 fig. 5c.

Thallus white, 2–8 cm broad, dull and finely granular; cortex lacking; algae scattered among superficial hyphae or subcortical; medulla mostly hypophloeodal; apothecia scattered, solitary or clumped in twos and threes, flush to semi-emergent, 0·4–0·6 mm diam, the thalline rim inconspicuous, entire to jagged, suberect, the exciple free apically, nearly filling the disc at maturity; disc pale tan to white pruinose; hymenium 40–90 μm; spores colourless, transversely septate, 4–5 × 12–20 μm, 5–8 loculate, I+.

CHEMISTRY. Stictic and constictic acids.

HABITAT. Saplings and lower trunks in rain forest at mid elevations (350–850 m).

DISTRIBUTION. West Indies, Central America, Sri lanka, Australia.

ADDITIONAL SPECIMENS. Hale collections: 1 (50 215A), 2 (51 226), 5 (46 250, 46 270, 46 278), 7b (50 306, 51 051, 51 057, 51 094), 8 (47 039, 47 048).

OBSERVATIONS. While the thalline rim is not reflexed, the disc is sufficiently open to justify placing the species in the '*T. platycarpum*' group. The free exciple fills the disc partially to completely, as noted by Müller Argoviensis. It is certainly related to *T. porinoides*, which has an incurved exciple and thalline rim with much larger spores. Both lack a cortex and contain stictic acid, and both are pantropical.

21. Thelotrema pidurutalagalum Hale **sp. nov.**
(Fig. 9c)

Thallus corticola, pro parte epiphloeodes, tenuis, rimosus, 2–3 cm latus; apothecia conspicua, urceolata, 0·6–0·8 mm diametro, excipulo libero, periphysoidibus instructis; ostiolum rotundatum, 0·15–0·3 mm diametro; hymenium 180–260 μm altum; sporae fuscae, transversim septatae, 12–21 × 90–100 μm, 15–18 loculatae, raro apice longitudinale 1–2 loculatae, 1–2 : nae, I−.

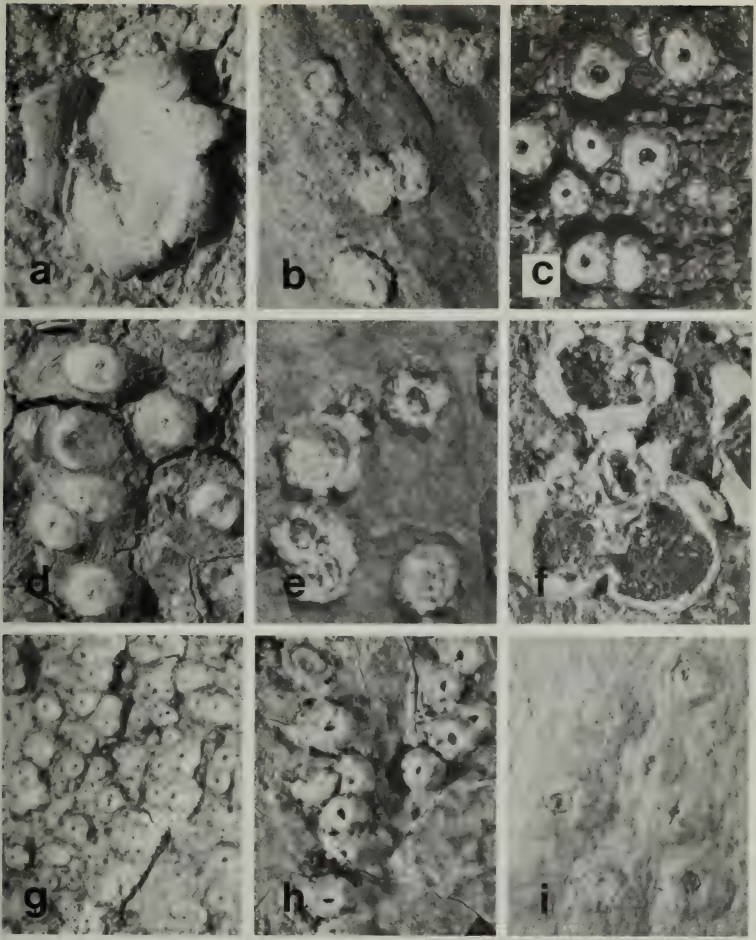

Fig. 9 Species of *Thelotrema*. (a) *T. patens* (Hale 50 254). (b) *T. phlyctidioides* (Hale 51 051). (c) *T. pidurutalagalum* (Hale 50 347). (d) *T. piluliferum* (Hale 50 340). (e) *T. platycarpoides* (Thwaites 634 in BM). (f) *T. platycarpum* (Thwaites C. L. 5 in BM). (g) *T. platysporum* (Hale 46 161). (h) *T. platysporum* (Hale 46 131). (i) *T. porinoides* (Hale 50 176). See Fig. 7i for scale.

Typus: Sri Lanka, Central Province, Nuwara Eliya District, Pidurutalagala, elev. 2520 m, 21 Mar. 1978, *M. E. Hale* 50 347 (US—holotypus).

Thallus whitish gray, 2–3 cm broad, dull, thin, fissured; cortex not clearly developed and probably lacking; algal layer more or less continuous among medullary hyphae; medulla 15–20 μm, with many crystals, mostly hypophloeodal; apothecia conspicuous, emergent and urceolate at maturity, 0·6–0·8 mm diam, the exciple free, pulling away from the wall with the disc, periphysoids present; pore gaping, 0·15–0·3 mm diam, white rimmed and eventually pruinose or decomposing; hymenium 180–260 μm; spores brown, transversely septate, 12–21 × 90–100 μm, 15–18 loculate, the ends occasionally 1–2 loculate longitudinally at maturity, 1–2/ascus, I−.

CHEMISTRY. No substances present.

HABITAT. On twigs of shrubs at high elevations (2520 m).

DISTRIBUTION. Sri Lanka.

ADDITIONAL SPECIMENS. Hale collections: 12 (50 352).

OBSERVATIONS. This species is closely related to *Thelotrema nostalgicum* (above) and *T. weberi* (below) in apothecial size and emergence as well as presence of periphysoids. It is the only species in the group lacking chemistry.

22. Thelotrema piluliferum Tuck. in *Proc. Am. Acad. Arts Sci.* **7** : 227 (1868).
(Fig. 9d)

Type: Hawaii, Oahu, Waialua Mtns, *Mann* s.n. (FH-Tuck.—lectotype; G, W—isolectotypes).

Thelotrema vernicosum Zahlbr. in *Annls mycol.* **10** : 370 (1912). Type: Hawaii, Koolau Mountains, *Rock* 101 (W—lectotype; FH—isolectotype)

Thelotrema gibbosum Magnusson in Magnusson & Zahlbr. in *Ark. Bot.* **31A**(1) : 53 (1944). Type: Hawaii, Maui, Haelaau, 1 Aug. 1938, *Selling* 5836 (UPS—lectotype; S—isolectotype).

Thallus light mineral gray, *c.* 8 cm broad, shiny, fissured; cortex dense, irregularly thickened, 5–10 μm, with some internal splitting; algal layer continuous, 15–20 μm; medulla 50–100 μm with crystals; apothecia numerous, emergent, rarely urceolate at maturity, 0·7–1·0 mm diam, the exciple fused, yellowish brown; pore tiny, *c.* 0·05 mm diam, often nearly closed, depressed; hymenium 140–160 μm; spores colourless, muriform, 8–12 × 24–28 μm, 1–3 × 4–6 loculate, uniseriate, I+.

CHEMISTRY. Psoromic acid.

HABITAT. Trees along trail at higher elevations (2200 m).

DISTRIBUTION. Sri Lanka, Sabah, Hawaii.

ADDITIONAL SPECIMENS. Hale collections: 12 (50 340).

OBSERVATIONS. The strongly emergent, tiny-pored apothecia resemble those of *Pertusaria*, as Tuckerman noted in his original description. Salisbury (1972*a* : 273) presumed it to be near *T. lepadinum* because of the periphysoids, as reported by Magnusson. As a matter of fact, Magnusson correctly identified *T. piluliferum* from Hawaii and still described *T. gibbosum* since it 'belonged to quite another group than the other Hawaiian species' because of the periphysoids. He evidently overlooked the periphysoids in Tuckerman's type.

Thelotrema piluliferum as delimited here has a fused exciple with dense short periphysoids, but differs considerably from the 'typical' species in the genus in having psoromic acid and a small pore, both characters more typical of *Myriotrema*, where one might be tempted to place it. *Thelotrema platysporum* (below) and *T. saxicola* (Vainio) G. Salisb. (Salisbury, 1972*a* : 269) share these anomalous characters. Three additional rare species have periphysoids and psoromic acid: poorly known *T. dislaceratum* Krempelh. from south-east Asia, *T. cryptotrema* Nyl. and *T. sphinctrinellum* Nyl. from tropical America.

23. Thelotrema platycarpoides Tuck. in *Proc. Am. Acad. Arts Sci.* **6** : 270 (1864). (Fig. 9e)

Type: Cuba, 17 Jan. 1863, *Wright* 157 (FH-Tuck.—lectotype; BM, H-Nyl. 22671, G, L, PC, UPS, US, W—isolectotypes).
Platygrapha bivela Berk. & Broome in *J. Linn. Soc.* (Bot.) **14** : 109 (1875). Type: Sri Lanka, *Thwaites* 634 (K—lectotype; BM—isolectotype).
Phaeotrema platycarpoides (Tuck.) Müll. Arg. in *Flora, Jena* **69** : 311 (1886).
ICONES. Salisbury, 1972*b* : 287 fig. 8.

Thallus pale tannish, 6–7 cm broad, thin, shiny; cortex dense, 15–18 μm, splitting internally; algal layer continuous, 15 μm; medulla 10–30 μm, with crystals; apothecia numerous, chroodiscoid, 0·5–1·2 mm diam, solitary or clustered in twos and threes, the thalline rim splitting and recurved, exciple free; disc open, rusty brown or becoming white pruinose at maturity; hymenium 60–70 μm; spores brown, transversely septate, 5–6 × 11–15 μm, 3–4 loculate, I−.

CHEMISTRY. Stictic and constictic acids.

HABITAT. Secondary forests at low elevations.

DISTRIBUTION. Mexico, West Indies, Sri Lanka, Java.

OBSERVATIONS. This species is well characterized by the chroodiscoid apothecia and chemistry. Tuckerman originally separated it from *T. platycarpum* because of the smaller apothecia (0·5–1·2 mm vs 1·0–2·5 mm diam) and somewhat larger spores. My own measurements on the types and other specimens, however, do not show any significant differences in spore size. Leighton added a note to the Thwaites collection of *Platygrapha bivela* in BM to the effect that it was a synonym of '*Thelotrema platycarpoides* Wright's Lich. Cubae 157' but the species was not included in his 1870 publication.

24. Thelotrema platycarpum Tuck. in *Proc. Am. Acad. Arts Sci.* **5** : 406 (1862). (Fig. 9f)

Type: Cuba, *Wright* 139 (FH-Tuck.—lectotype; BM, H-Nyl. 22668, G, L, UPS, US—isolectotypes).
Asteristion erumpens Leighton in *Trans. Linn. Soc. Lond.* **27** : 163 (1870). Type: Sri Lanka, Central Province, *Thwaites* C. L. 5 (BM—lectotype; H-Nyl. 22683, S, UPS—isolectotypes) (as 'Lgt. 22, *Asteristion erumpens*').
Platygrapha albo-rufa Berk. & Broome in *J. Linn. Soc.* (Bot.) **14** : 110 (1875). Type: Sri Lanka, *Thwaites* 69 (K—lectotype).
Phaeotrema platycarpum (Tuck.) Zahlbr., *Cat. Lich. Univers.* **2** : 609 (1923).
Phaeotrema erumpens (Leighton) Santesson in *Symb. bot. upsal.* **12**(1) : 423 (1952).
Phaeotrema apertum C. Dodge in *Beih. nov. Hedwigia* **12** : 98 (1964). Type: Uganda, Mulange Forest, *Dümmer* 4293 (BM—holotype).
ICONES. Salisbury, 1972*b* : 286 fig. 7.

Thallus dark tannish, *c.* 4 cm diam, dull; cortex dense, 15-18 μm, splitting somewhat internally; algal layer continuous, to 30 μm; medulla to 30 μm, with some crystals; apothecia conspicuous, solitary or aggregated, 1–2·5 mm diam, chroodiscoid, the thalline margin splitting and strongly recurved, the inner wall white pruinose, the exciple free, erect; disc variable, tan to rusty brown or heavily white pruinose; hymenium 60–75 μm; spores brown, transversely septate, 4–6 × 9–14 μm, 4-loculate, often shrivelling at maturity, I—.

CHEMISTRY. Stictic and constictic acids.

HABITAT. Secondary forests at lower elevations.

DISTRIBUTION. United States, West Indies, Uganda, Sri Lanka, Sarawak, Java.

OBSERVATIONS. The large chroodiscoid apothecia are very conspicuous. The differences with

T. platycarpoides are given above. I did not recollect either species in the rain forest; they occur in semi-arid secondary habitats.

25. Thelotrema platysporum Harm. in *Bull. Séanc. Soc. Sci. Nancy* III, **13** : 41 (1912).
(Fig. 9g, h)

Type: New Caledonia, *Pionniero* 38 (DUKE—lectotype; FH, W—isolectotypes).

Thelotrema diminitum Hale in *Phytologia* **27** : 494 (1974). Type: Sarawak, Bako National Park, 10 Mar. 1965, *M. E. Hale* 30 536 (US—holotype) ('platysporum' unknown present but psoromic acid lacking).

ICONES. Hale, 1974*b* : 500 fig. 11.

Thallus whitish or greenish ashy, 6–16 cm broad, shiny, smooth, continuous; cortex dense, thin, 5–10 μm, with aculeate hyphae, splitting and exfoliating; algal layer partially interrupted by crystals, 10–25 μm; medulla 10–110 μm with crystals and cortical inclusions; apothecia numerous, emergent, 0·3–0·7 mm diam, solitary or grouped in twos and threes, the exciple fused, colourless, with short periphysoids; pore very small, 0·03–0·05 (–0·15) mm diam, the surrounding area often crumbling, narrowly black rimmed; hymenium 90–120 μm; spores colourless, muriform, 7–12 × 14–30 μm, 1–2 × 4–5 loculate, uniseriate, I+.

CHEMISTRY. Unidentified substance above atranorin in t.l.c. plates, with or without psoromic acid (confirmed by Dr C. F. Culberson).

HABITAT. Over mosses and bark on canopy branches in rain forest at low elevations (300 m).

DISTRIBUTION. Sri lanka, Sarawak, New Caledonia, Australia.

ADDITIONAL SPECIMENS. Hale collections: 1 (50 249), 2 (51 136), 4 (47 053, 47 057, 47 077, 47 121, 47 130, 47 161, 50 384, 50 446, 50 466, 50 482), 6 (47 208), 7a (50 156, 50 190), 7b (50 302, 51 079), 9 (46 131, 46 172). Thwaites collections: C. L. s.n. (PDA), C. L. 31 (BM, H-Nyl. 22 556) (as 'Lgt. 85. *T. punctulatum*'), C. L. 99 (BM, H-Nyl. 3880, S, UPS) (as 'Lgt. 77. *T. sphinctrinellum*'), C. L. 174 (BM) (mixed with *Myriotrema terebratulum*) (as 'Lgt. 87 *T. myriotrema*').

OBSERVATIONS. *Thelotrema platysporum* is an extremely variable species characterized by the unknown chemistry and the semi-emergent to emergent apothecia with a fused, periphysoid-bearing exciple. The pore area varies from entire and distinctly annulate to 'decomposed' as the rim seems to disintegrate and become lined with protruding excipular material. Overall the apothecial structure is similar to that of *T. piluliferum* and these two species are probably very closely related. *Thelotrema platycarpum* is one of the commonest members of the genus in Sri Lanka.

Leighton identified the Thwaites collection C. L. 99 as '*T. sphinctrinellum* Nyl.' although Nylander marked his duplicate 'false determinato'. The type of this species from Colombia (H-Nyl. with isotypes in FH-Tuck. and PC) has 4-loculate spores and contains psoromic acid. Re-examination of these collections led me to conclude that *Ocellularia lopezii* Hale, which I described from Venezuela (Hale, 1975 : 174), is a synonym of *Thelotrema sphinctrinellum.*

26. Thelotrema porinoides Mont. & Bosch in Junghuhn, *Enum. Pl. Insul. Java Sumatra* : 151 (1855).
(Fig. 9i)

Type: Java, *Junghuhn* 151 (L—lectotype; FH-Tuck., G, PC, W—isolectotypes).

Thelotrema exanthismocarpum Leighton in *Trans. Linn. Soc. Lond.* **27** : 169 (1870). Type: Sri lanka, Central Province, *Thwaites* C. L. 97 (BM—lectotype).

Thelotrema albidiforme Leighton in *Trans. Linn. Soc. Lond.* **27** : 170 (1870). Type: Sri Lanka, *Thwaites* C. L. 19 (BM—lectotype; PDA—isolectotype).

Ocellularia albidiformis (Leighton) Zahlbr. in *Annls mycol.* **14** : 50 (1916).

Ocellularia exanthismocarpa (Leighton) Zahlbr., *Cat. Lich. Univers.* **2** : 590 (1923).
For additional synonymy see Hale (1974*a* : 20).
ICONES. Hale, 1974*a* : 21 fig. 11c (lectotype).—Hale, 1978*a* : 18 fig. 51.—Salisbury, 1972*a* : 265 fig. 2.

Thallus whitish to pale greenish, 2–8 cm broad, dull, continuous; cortex lacking; algal layer scattered in patches of superficial medullary hyphae; medulla mostly hypophloeodal but often developed near the apothecia; apothecia common, solitary or aggregated in twos or threes, more or less immersed to semi-emergent, to 0·7 mm diam, the thalline wall sometimes flaring, the exciple free but distinctly incurved to form an inner pore; pore round, 0·2–0·4 mm diam; hymenium *c.*180 μm; spores colourless, transversely septate, 8–15 × 60–125 μm, 26–29 loculate, I+.

CHEMISTRY. Stictic and constictic acids, rarely accompanied by the higher 'quintaria' spot (Hale, 1974*a* : 12).

HABITAT. Tree trunks along trails at 150–2000 m elevation.

DISTRIBUTION. West Indies, Central America, India, Sri Lanka, Philippines, Java, Sabah, Solomon Islands, Hawaii.

ADDITIONAL SPECIMENS. Hale collections: 1 (50 200, 50 202, 50 213), 2 (51 181), 3a (46 300, 46 304), 5 (46 229), 7a (50 176, 50 188), 8 (47 029), 9 (46 198), 10 (50 263). Thwaites collections: C. L. 97 (BM, H-Nyl. 3855) (as 'Lgt. 91, *Thelotrema exanthismocarpum*'; PDA material is *Ocellularia stictidea*).

OBSERVATIONS. The double pore, resulting from the distinct, incurved exciple, has been noted by the various authors who studied the species under its numerous synonyms. We cannot be sure why Leighton described *Thelotrema albidiforme* since the description is virtually identical with that of *T. exanthismocarpum*. The scant thallus is 'lutescens' since the underlying bark substrate is olive brown in contrast to the whitish bark ('albido-fuscescens') on which the type of *T. exanthismocarpum* was growing. In any event I proved stictic acid in both collections with t.l.c.

Salisbury (1972*a* : 265) places *Ocellularia obovata* (Stirton) Zahlbr. in synonymy under *Thelotrema porinoides*. The type of *T. obovatum* from New Zealand (BM), however, is corticate, has no inner ring formed by the exciple, and lacks lichen substances.

27. Thelotrema pseudoexanthismocarpum (Patw. & C. Kulk.) Hale in *Mycotaxon* 11 : 132 (1980).

(Fig. 10a)

Ocellularia pseudoexanthismocarpa Patw. & C. Kulk. in *Norw. J. Bot.* **24** : 130 (1977). Type: India, Kerala, Anamalai Hills, *M. B. Nagarkar & K. D. Gole* 76·308 (AMH—holotype).
ICONES. Patwardhan & Kulkarni, 1977 : 129 fig. 7.

Thallus light yellowish brown, 6–10 cm broad, dull; cortex very dense, 20–30 μm; algal layer continuous, 15–20 μm; medulla to 30 μm with crystal inclusions, mostly hypophloeodal; apothecia numerous, conspicuous, solitary to aggregated, 1–1·2 mm diam, the thalline rim coarse, erect to nearly recurved, apically lacerated, exciple free, coarse, partially filling the disc; pore round, *c.* 0·1 mm diam but usually lost in the mass of excipular material; hymenium 190–200 μm; spores colourless, transversely septate, 12–20 × 80–150 μm, 12–15 loculate, 2/ascus, I+.

CHEMISTRY. No substances present.

HABITAT. Lower bole to canopy trees in rain forest at lower elevations (150–800 m).

DISTRIBUTION. India, Sri Lanka.

ADDITIONAL SPECIMENS. Hale collections: 1 (50 223), 3a (46 338), 4 (47 115, 50 404), 7b (51 017), 8 (47 040), 9 (46 165).

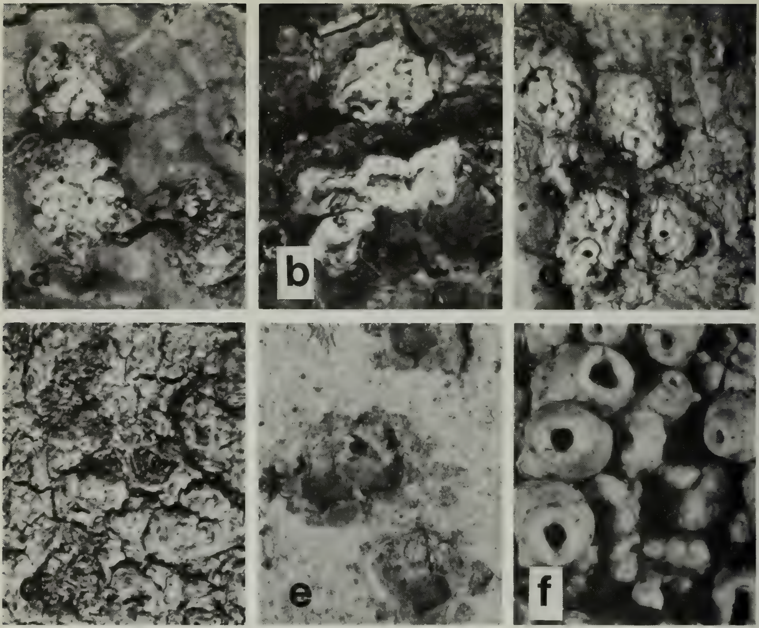

Fig. 10 *Species of Thelotrema.* (a) *T. pseudoexanthismocarpum* (Hale 47 040). (b) *T. pulvereodiscum* (Hale 47 064). (c) *T. scabiomarginatum* (Hale 46 265). (d) *T. subpatens* (Hale 46 208). (e) *T. waasii* (Hale 51 175). (f) *T. weberi* (Santesson 25 980 in US). See Fig. 7i for scale.

Observations. *Ocellularia pseudoexanthismocarpa* was first described from India and represents another rare example of the Sri Lanka–India distribution pattern. In spite of the epithet it differs significantly from *Thelotrema porinoides* in having a distinct cortex and in lacking chemical substances, although the presence of periphysoids places them in a close ontogenetic relationship. The specimens from Sri Lanka have larger apothecia than the Indian type (Fig. 11g) but preserve the same round, distinct pore within the mass of excipular material. Externally it is very similar to *Thelotrema scabiomarginatum* (see below).

28. Thelotrema pulvereodiscum Hale sp. nov.
(Fig. 10b)

Thallus corticola, epiphloeodes, albo-cinereus, opacus, aetate rimosus, 8–10 cm latus; apothecia dispersa, chroodiscoidea, rotundata vel irregulariter elongata, 0·8–1·1 mm diametro, margine thallino erecto, sorediato, excipulo libero, periphysoidibus instructis, disco nigro vel albo-pruinoso; hymenium 60–90 μm altum; sporae fuscae, murales, octonae, 4 × 9–10 μm, 1–2 × 3–4 loculate, I−.

Typus: Sri Lanka, Sabaragamuwa Province, Ratnapura District, Sinharaja Forest Reserve near Weddagala, elev. 300 m, 13 Feb. 1976, *M. E. Hale* 47 064 (US—holotypus).

Thallus whitish gray, 8–10 cm broad, thin, dull, fissuring with age; cortex very thin, 5–7 μm; algal layer continuous, 10–15 μm; medulla 10 μm or less, mostly hypophloeodal; apothecia dispersed, chroodiscoid, round to irregularly elongate, 0·8–1·1 mm, thalline rim low, suberect, becoming sorediate at tips and on the inner side, exciple free, thick, partially filling the disc, periphysoids present; disc blackish or white pruinose; hymenium 60–90 μm; spores brown, muriform, 4 × 9–10 μm, 1–2 × 3–4 loculate, shriveling at maturity, I—.

CHEMISTRY. Stictic and constictic acids.

HABITAT. Canopy of trees in rain forest at lower elevations (300 m).

DISTRIBUTION. Sri Lanka.

OBSERVATIONS. Brown-spored, chroodiscoid species of *Thelotrema* are very rare; I know of only two others, *Thelotrema mirabile* (Zahlbr.) Hale, a species from Taiwan first described under *Phaeographina*, characterized by a very broad disc (3 mm diam) and larger spores (42–46 μm long), and *T. stellatum* (Hale) Hale (see Hale, 1978*a* : 54), which has very large spores (to 120 μm long) and no chemistry.

29. **Thelotrema scabiomarginatum** Hale **sp. nov.**
(Fig. 10c)

Thallus corticola, epiphloeodes, viridi-cinerascens, 8–15 cm latus; apothecia immersa, 0·6–1·5 mm diametro, margine thallino erecto, exciputo libero, crasso, periphysoidibus instructis, columella nulla; hymenium 120–210 μm altum; sporae incolores, murales, 10–20 × 50–180 μm, dense cellulares, 1–4 : nae, I–.

Typus: Sri Lanka, Southern Province, Matara District, mossy forest above Enselwatta, elev. 1100 m, 14 Feb. 1976, *M. E. Hale* 46 240 (US—holotypus; BM—isotypus).

Thallus light greenish to tannish gray, 8–15 cm broad, shiny, continuous or fissured; cortex dense, 12–20 μm, with aculeate hyphae; algal layer continuous, 10–15 μm; medulla mostly hypophloeodal; apothecia conspicuous, immersed, chroodiscoid, 0·6–1·5 mm diam, solitary or aggregated in twos, the thalline rim becoming erect, apically broadened and crumbling, exciple free, partially or completely filling the disc, periphysoids present, pore round, 0·1 mm diam but often lost in the erupting mass of excipular material; hymenium 120–210 μm; spores colourless, muriform, 10–20 × 50–180 μm, becoming densely celled, 1–4/ascus, I+.

CHEMISTRY. No substances present.

HABITAT. Base and lower trunk of trees in rain forest at low to mid elevations (150–850 m).

DISTRIBUTION. Sri Lanka.

ADDITIONAL SPECIMENS. Hale collections: 1 (50 240, 50 253), 2 (51 105), 3a (46 293, 46 312), 4 (47 065, 47 091, 47 162, 50 432, 50 453, 50 475, 50 519), 5 (46 245, 46 265), 9 (46 170, 46 173, 46 211).

OBSERVATIONS. This endemic species is very close to *T. pseudoexanthismocarpum* in the development of large, erumpent apothecia. The spores are often poorly developed, and some of my identifications were made on the basis of apothecial structure only.

30. **Thelotrema subpatens** Hale **sp. nov.**
(Fig. 10d)

Thallus corticola, pro parte hypophloeodes, continuus, albo-cinereus, 8–12 cm latus; apothecia subemersa, 0·5–0·8 mm diametro, margine thallino suberecto, exciputo libero, periphysoidibus instructis, disco aperto; hymenium 60 μm latum; sporae incolores, transversim septatae, 5–6 × 24–25 μm, 7–8 loculatae, I+ coeruleae.

Typus: Sri Lanka, Southern Province, Galle District, Kanneliya Forest Reserve, elev. 150 m, 16 Feb 1976, *M. E. Hale* 46 208 (US—holotypus; BM—isotypus).

Thallus whitish mineral gray, 8–12 cm broad, shiny, continuous; cortex barely discernible and probably not developed; algae scattered among superficial medullary hyphae; medulla to 25 μm in patches, mostly hypophloeodal; apothecia immersed to barely raised, 0·5–0·8 mm diam, the thalline rim erect to barely recurved, the exciple free, partially filling the disc, periphysoids present; hymenium 60 μm; spores colourless, transversely septate, 5–6 × 24–26 μm, 7–8 loculate, I+.

CHEMISTRY. No substances present.

HABITAT. Lower trunks in rain forest at low elevations (150 m).

DISTRIBUTION. Sri Lanka.

OBSERVATIONS. This species is represented only by the type specimen. There are no close relatives, except perhaps *T. pycnophragmium* Nyl., which has larger, muriform spores.

31. **Thelotrema waasii** Hale **sp. nov.**
(Fig. 10e)

Thallus corticola, hypophloeodes, opacus, albidus, 2–3 cm latus; apothecia conspicua, chroodiscoidea, disco late aperto, 1–1·5 mm diametro, margine thallino valde recurvato, fisso, onmino purpureo, exciplo connato, periphysoidibus instructis; hymenium 65–70 μm altum; sporae incolores, transversim septatae, octonae, 5 × 15–18 μm, 5–6 loculatae, I–.

Typus: Sri Lanka, Sabaragamuwa Province, Ratnapura District, Halwathura-Kanda, near Rassagala, elev. 850–900 m, 15 Mar. 1978, *M. E. Hale* 51 175 (US—holotypus).

Thallus white, 2–3 cm broad, dull, continuous; cortex lacking; algae scattered among superficial medullary hyphae; medulla mostly hypophloeodal; apothecia chroodiscoid, very conspicuous, 1–1·5 mm diam, the thalline rim strongly emergent, split and recurved, coarse, the exciple fused, with short periphysoids; disc and inner thalline wall deep violet purple K+ dark purple; hymenium 65–70 μm; spores colourless, tranversely septate, 5 × 15–18 μm, 5–7 loculate, I–.

CHEMISTRY. No medullary substances present; unidentified purple pigment K+ purple.

HABITAT. Branch of sapling in rain forest at mid elevation (900 m).

DISTRIBUTION. Sri Lanka.

OBSERVATIONS. *Thelotrema waasii* resembles *T. dilatatum* (above) in many respects: the large apothecia with recurved thalline rim, fused exciple, and lack of cortex. It differs in the brilliantly coloured disc, smaller spores, and lack of stictic acid. It is named in honour of Shelton Waas, whose logistical help was crucial during my excursions in Sri Lanka.

32. **Thelotrema weberi** Hale in *Phytolgia* **27** : 497 (1974).
(Fig. 10f)

Type: New Guinea, Papua, Eastern Highlands, 1 July 1968, *Weber & McVean* 48 666 (COLO—holotype; US—isotype).
ICONES. Hale, 1974*b* : 501 fig. 18.

Thallus light brownish ashy, *c.* 6 cm broad, shiny, continuous; cortex probably lacking or remaining as a polysaccharide covering; algal layer 15–30 μm; medulla 60–100 μm, with large crystals; apothecia conspicuous, emergent and urceolate, 1–1·5 mm diam and to 2 mm high, the exciple free, forming an interior ring; pore gaping, 0·3–0·8 mm diam, white rimmed; hymenium 250–290 μm; spores colourless, muriform, 15–35 × 150–190 μm, densely celled, 1–2/ascus, I+.

CHEMISTRY. Norstictic acid.

HABITAT. On cultivated trees (*Cupressus*) at high elevations (2100 m).

DISTRIBUTION. Sri Lanka, Sabah, New Guinea.

ADDITIONAL SPECIMENS. Nuwara Eliya District, *Santesson* 25 890 (S), *Wheeler* 12 376, 12 379 (US).

Observations. Other comparable periphysoid-bearing species with large urceolate apothecia include *T. nostalgicum* and *T. pidurutalagalum*, all found at higher elevations. They form a close phylogenetic group in spite of the spore differences.

II. MYRIOTREMA Fée

Essai Crypt. XLIX (1824).
Coscinedia Massal. in *Atti R. Ist veneto Sci.* III, **5** : 256 (1860).

Thallus crustose, epiphloeodal; cortex usually dense with splitting and exfoliation, more rarely loosely organized or lacking; medulla well developed; apothecia either immersed in the medulla without development of a thalline rim, less commonly immersed in the periderm, or raised with a distinct incurved thalline rim and a tiny pore; exciple colourless to reddish brown, lacking periphysoids, usually fused; spores colourless or brown, transversely septate or muriform, I+ deep blue or rarely I−.

Type species. *Myriotrema olivaceum* Fée.

Number of species. About 150.

Observations. The main nucleus of the genus, comprising 21 of the species in Sri Lanka related to *M. olivaceum*, have apothecia immersed in the medulla, 0·2–0·4 mm diam, and flush with the surface: *M. album, M. compunctum, M. decorticatum, M. fissurinum, M. frondosum, M. glaucescens, M. hartii, M. microporum, M. minutum, M. multicavum, M. nuwarense, M. olivaceum, M. polytretum, M. protoalbum, M. rugiferum, M. santessonii, M. subconforme, M. terebrans, M. terebratulum, M. thwaitesii,* and *M. wightii.* Six other species, *M. albocinctum, M. anamalaiense, M. andamanicum, M. masonhalei, M. mastarion,* and *M. minutulum,* are deeply immersed in the periderm.

The remaining species in Sri Lanka have raised apothecia which externally seem more related to *Ocellularia* than to *Myriotema: M. cinereoglaucescens, M. costaricense, M. desquamans, M. elachistoteron, M. eminens, M. fluorescens, M. glaucophaenum, M. granulosum, M. microstomum,* and *M. porinaceum.* They differ from *Ocellularia,* of course, in lacking a carbonized exciple. Only detailed ontogenetic studies, however, can demonstrate eventually whether *Myriotrema* as presently conceived is a polyphyletic group.

Salisbury (1978) recognized the difference in emergence by dividing the species that he had examined into two groups under *Thelotrema* sect. *Myriotrema,* the '*T. album*' group (apothecia immersed) and the '*T. bahianum*' group (apothecia raised). I have not tried to organize the Sri Lankan species along these lines.

Key to the species

1	Spores colourless	2
–	Spores brown	32
2	Spores tranversely septate	3
–	Spores muriform	21
3	Spores large, 90–150 µm; medulla pale yellow	17. **M. granulosum**
–	Spores small, less than 30 µm long; medulla white	4
4	Apothecia deeply immersed in the periderm	5
–	Apothecia immersed in the medulla with little or no periderm inclusions or somewhat raised	7
5	Medulla P− (no substances present)	1. **M. albocinctum**
–	Medulla P+ yellow or orange	6
6	Medulla P+ yellow (psoromic acid present)	23. **M. minutulum**
–	Medulla P+ orange ('thwaitesii' unknown present)	36. **M. thwaitesii**
7	Medulla conspicuous, 150–300 µm thick	8
–	Medulla comparatively thin, 10–60 µm thick	13
8	Thallus conspicuously fissured (without magnification)	9
–	Thallus continuous, fissured only with age	10

9 Medulla P+ yellow (psoromic acid) . . . . 21. **M. microporum**
– Medulla P— ('olivacea' unknown) . . . . 27. **M. olivaceum**
10 Pore very tiny, 0·05 mm diam; medulla P+ red (fumarprotocetraric acid) 24. **M. minutum**
– Pore about 0·1 mm diam; medulla P— or P+ yellow 11
11 Medulla P— ('olivacea' unknown) . . . . 27. **M. olivaceum**
– Medulla P+ yellow (psoromic acid) 12
12 Thallus surface grainy, friable; medulla with dense crystal inclusions 25. **M. multicavum**
– Thallus smooth, continuous, not friable; crystal inclusions not dense 35. **M. terebratulum**
13 Apothecia raised, large, 0·7–1·0 mm diam; pore 0·4–0·7 mm diam . 7. **M. costaricense**
– Apothecia immersed to flush, less than 0·5 mm diam; pore 0·05–0·1 mm diam . . 14
14 Medulla P— (no substances present) 15
– Medulla P+ yellow or orange 17
15 Apothecia somewhat raised, 0·3–0·5 mm diam . . . . 5. **M. cinereoglaucescens**
– Apothecia flush, 0·1–0·4 mm diam 16
16 Thallus pale whitish green; pore 0·1 mm diam . . . . 2. **M. album**
– Thallus dark olive green; pore 0·01 mm diam . . . . . 30. **M. protoalbum**
17 Stictic acid present on t.l.c. . . . . 34. **M. terebrans**
– Psoromic acid or 'thwaitesii' unknown present 18
18 Psoromic acid present on t.l.c. 19
– 'Thwaitesii' unknown present on t.l.c 20
19 Thallus 50–200 μm thick; apothecia flush . . . . . . 25. **M. terebratulum**
– Thallus less than 100 μm thick; apothecia somewhat raised at maturity . . . . .
16. **M. glaucophaenum**
20 Thallus dull; apothecia partially immersed in periderm . . . 36. **M. thwaitesii**
– Thallus shiny; apothecia immersed in medulla only . . . . . 28. **M. polytretum**
21 Thallus isidiate to pustulate 22
– Thallus smooth to verruculose, lacking isidia and pustules 24
22 Isidia pustular, erupting apically . . . . 32. **M. santessonii**
– Isidia solid and cylindrical or flattened, not pustular 23
23 Isidia cylindrical, coarse . . . . 18. **M. hartii**
– Isidia flattened, leaf-like . . . . 14. **M. frondosum**
24 Apothecia elongate at maturity; lichexanthone present (thallus orange under ultraviolet light) . . . . 13. **M. fluorescens**
– Apothecia round; lichexanthone lacking 25
25 Spores large, 100–250 μm long 26
– Spores small to medium sized, 20–75 μm long 29
26 Apothecia distinctly emergent 27
– Apothecia immersed and flush to barely raised 28
27 Apothecia becoming urceolate, 0·4–0·5 mm diam . . . . . . 11. **M. eminens**
– Apothecia not becoming urceolate, about 1 mm diam . . . . 22. **M. microstomum**
28 Apothecia deeply immersed in periderm, flush; medulla P+ yellow (psoromic acid) .
19. **M. masonhalei**
– Apothecia immersed in the medulla, becoming somewhat raised at maturity; medulla P+ orange (norstictic acid present) . . . . 29. **M. porinaceum**
29 Apothecia deeply immersed in periderm; spores to 75 μm long . 3. **M. anamalaiense**
– Apothecia immersed in the medulla; spores less than 20 μm long 30
30 Thallus with sparse, blunt isidia . . . . 18. **M. hartii**
– Isidia lacking 31
31 Medulla P+ yellow (psoromic acid) . . . . 31. **M. rugiferum**
– Medulla P– (no substances present) . . . . 33. **M. subconforme**
32 Spores transversely septate only . . . . 20. **M. mastarion**
– Spores muriform 33
33 Apothecia deeply immersed in periderm; thallus P+ yellow (psoromic acid) . . .
4. **M. andamanicum**
– Apothecia immersed in the medulla; thallus P+ orange (stictic acid) or P— 34
34 Spores large, 45–90 μm 35
– Spores small, 10–33 μm 36
35 Thallus surface grainy and finely verruculose; pore 0·05–0·1 mm diam 10. **M. elachistoteron**
– Thallus surface smooth and continuous; pore 0·1 mm diam or more . 26. **M. nuwarense**

36 Medulla thick and columnar, 150–600 μm 37
– Medulla less than 100 μm thick, not columnar 39
37 Medulla usually containing small masses of red crystals, P– . . 37. **M. wightii**
– Medulla white, lacking red crystals, P+ orange (stictic or norstictic acids present) . . 38
38 Apothecia round; norstictic acid present on t.l.c. . . . . . 6. **M. compunctum**
– Apothecia angular; stictic acid present on t.l.c. . . . . . . 15. **M. glaucescens**
39 Cortex and medulla sometimes lacking away from apothecia; pore area darkened . . 8. **M. decorticatum**
– Cortex and medulla distinct, uniformly developed; pore area concolourous or white . 40
40 Apothecia 0·3–0·4 mm diam, raised at maturity . . . . . . 9. **M. desquamans**
– Apothecia 0·2–0·3 mm diam, flush at maturity . . . . . . 12. **M. fissurinum**

1. **Myriotrema albocinctum** Hale **sp. nov.**

(Fig. 11a)

Thallus corticola, epiphloeodes, minute verrucosus, nitidus, pallide albo- vel viridi-cinereus, 8–12 cm latus; apothecia dispersa, immersa, 0·3–0·4 mm diametro, columella nulla; ostiolum rotundatum, 0·05–0·1 mm diametro, vix annulatum; hymenium *c.* 90 μm altum; sporae octonae, 5–6 × 16–30 μm, 5–8 loculatae, I+ coeruleae.

Typus: Sri Lanka, Sabaragamuwa Province, Ratnapura District, Gilimale Forest Reserve, elev. 150 m, 12 Feb. 1976, *M. E. Hale* 46 331 (US—holotypus)

Thallus pale greenish to whitish gray, 8–12 cm broad, the surface smooth to finely verruculose, continuous; cortex dense, 8–10 μm, with aculeate hyphae; algal layer continuous, 10 μm; medulla 10–20 μm; apothecia deeply immersed in the periderm, 0·3–0·4 mm diam, the exciple fused, apically reddish brown, columella lacking; pore round, 0·05–0·08 mm diam, white rimmed; hymenium 90–140 μm; spores colourless, transversely septate, 5–6 × 16–30 μm, 5–8 loculate, I+.

CHEMISTRY. No substances present.

HABITAT. Base and lower level, saplings, rarely into the canopy, in rain forest at lower elevations (150–450 m).

DISTRIBUTION. Sri Lanka.

ADDITIONAL SPECIMENS. Hale collections: 4 (47 099); 6 (47 180, 47 182), 7a (50 146, 50 168), 7b (50 298, 50 314, 51 009, 51 242), 8 (47 028), 9 (46 182).

OBSERVATIONS. The deeply sunken apothecia are characteristic of this species, so far known only from Sri Lanka. It is related to the psoromic acid-containing *M. minutulum*.

2. **Myriotrema album** Fée, *Ess. Crypt.* : 104 (1824).

(Fig. 11b)

Type: South America (?), on *Bonplandia trifoliata* (G—lectotype; H-Nyl. 22 635, isolectotype).
Thelotrema album (Fée) Nyl. in *Annls Sci. nat.* (Bot.) V, **7** : 315 (1867).
Ocellularia alba (Fée) Müll. Arg. in *Mém. Soc. Phys. Hist. nat. Genève* **29**(8) : 6 (1887).
See Hale (1978*a* : 12) for additional synonymy.
ICONES. Redinger (1936 : 44) fig. 20; Salisbury (1978 : 411) fig. 5; Hale (1978*a* : 3, 13) figs lc (lectotype) and 4b.

Thallus pale greenish gray, 6–10 cm broad, the surface shiny, smooth, somewhat fissured with age; cortex cellular, dense, 10–20 μm, with aculeate hyphae, splitting with some exfoliating layers; algal layer continuous, 12 μm; medulla to 30 μm thick with large dispersed crystals, mostly hypophloeodal; apothecia numerous, immersed in the medulla, 0·2–0·4 mm diam, the exciple mostly fused with only the tips free, pale reddish brown, prominent to barely visible within the pore; pore round, 0·1–0·15 mm diam, rarely white rimmed and more or less raised; hymenium 70–80 μm; spores colourless, transversely septate, 4–6 × 9–15 μm, 4-loculate, I+.

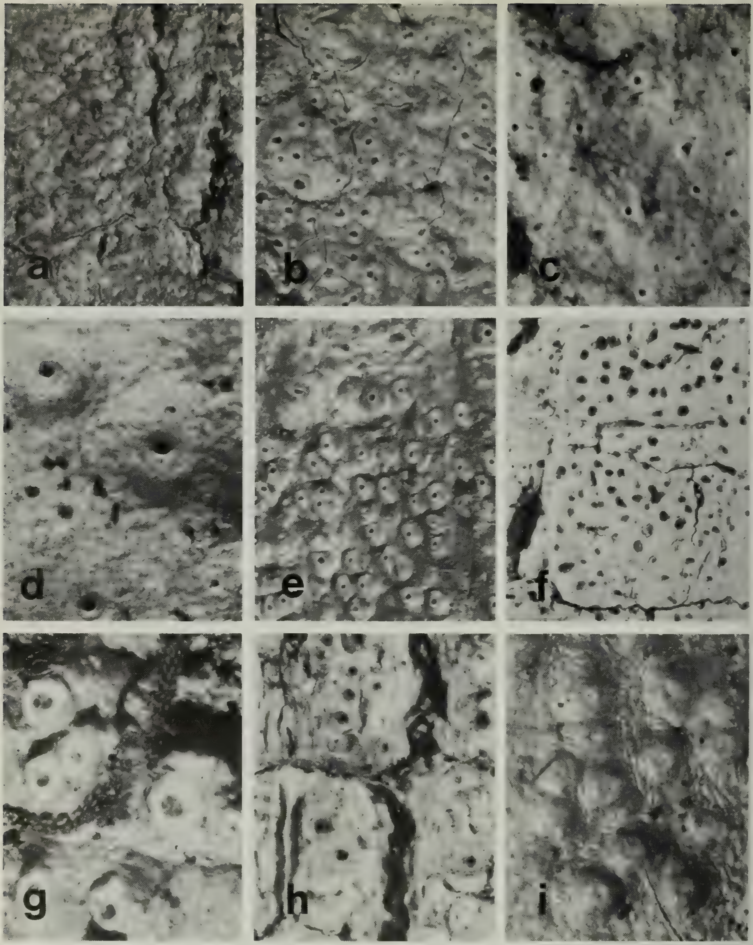

Fig. 11 Species of *Myriotrema*. (a) *M. albocinctum* (Hale 46 331). (b) *M. album* (Hale 46 190). (c) *M. anamalaiense* (Hale 46 220). (d) *M. andamanicum* (Hale 51 016). (e) *M. cinereoglaucescens* (Hale 46 363). (f) *M. compunctum* (Hale 51 033). (g) *M. costaricense* (Hale 46 143). (h) *M. decorticatum* (Hale 46 259). (i) *M. desquamans* (Hale 47 209). See Fig. 7i for scale.

CHEMISTRY. No lichen substances present.

HABITAT. Mid bole to canopy at lower elevations in rain forest (150–300 m).

DISTRIBUTION. West Indies, Central and South America, Philippines, Sarawak, Solomon Islands, Australia.

ADDITIONAL SPECIMENS. Hale collections: 4 (47 068, 47 078), 9 (46 171, 46 190).

OBSERVATIONS. *Myriotrema album* has a thin thallus, usually a rimless pore, and no lichen substances. The other confusable species, which occupy the same habitats and elevational range, have thalli 200–300 μm thick and different chemistry: *M. microporum* and *M. terebratulum* with psoromic acid and *M. olivaceum* with the 'olivacea' unknown.

In my study of the Thelotremataceae of Panama I considered *Thelotrema myrioporum* Tuck. to be a synonym of *Ocellularia (Myriotrema) alba*. As Tuckerman and later Redinger (1936 : 42) discovered, this species has consistently 2-loculate spores, a fact I have confirmed both in the type (FH-Tuck.) and in Redinger's Malme collections (S). What I have identified as *M. album* always has 4-loculate spores, feeling that septation alone is not a strong character since other biloculate species (e.g. *M. uniseptatum* (Hale) (Hale, 1978*a* : 33) may have occasional 3-loculate spores. It is probably better, however, to recognize *M. myrioporum* as a distinct species.

3. Myriotrema anamalaiense (Patw. & C. Kulk.) Hale in *Mycotaxon* **11** : 132 (1980).
(Fig. 11c)

Thelotrema anamalaiense Patw. & C. Kulk. in *Norw. J. Bot.* **24** : 127 (1977). Type: India, Kerala, Anamalai Hills, *Patwardhan & Kulkarni* 76. 344 (AMH—holotype; US—isotype).

Thallus pale tannish gray, *c.* 8 cm broad, smooth, continuous; cortex loosely organized, 10–18 μm, irregularly pored; algal layer 10–15 μm; medulla 30–60 μm with numerous crystals; apothecia immersed in the periderm, 0·3–0·5 mm diam, exciple partially free, usually visible as an inner ring through the pore; pore round, 0·1–0·2 mm diam, depressed at maturity, white rimmed; hymenium 150–170 μm; spores colourless, muriform, 15–20 × 70–75 μm, 2–4 × 12–15 loculate, 2–4/ascus, I+.

CHEMISTY. Stictic and constictic acids.

HABITAT. Lower trunks of trees in rain forest at mid elevations (1100 m).

DISTRIBUTION. India, Sri Lanka.

ADDITIONAL SPECIMENS. Hale collections: 5 (46 220).

OBSERVATIONS. This species is distinguished by the immersed apothecia, large spores, and chemistry. Externally it resembles *M. andamanicum,* which has small brown muriform spores and psoromic acid.

4. Myriotrema andamanicum (Nyl.) Hale in *Mycotaxon* **11** : 132 (1980).
(Fig. 11d)

Thelotrema andamanicum Nyl. in *Bull. Soc. linn. Normandie* II, **7** : 167 (1873). Type: India, Andaman Islands, 1867, *Kurz* s.n. (H-Nyl. 22 455—lectotype).
Leptotrema andamanicum (Nyl.) A. L. Sm. in *J. Linn. Soc. Lond.* **46** : 74 (1922).

Thallus pale tannish gray, 6–8 cm broad, shiny, continuous; cortex loosely organized, 10–15 μm; algal layer continuous, 10–15 μm; medulla 10–30 μm, with dense crystals, mostly hypophloeodal; apothecia deeply immersed in the periderm, 0·8–1·1 mm diam, the exciple fused, pale reddish brown; pore round, 0·1–0·2 mm diam, with a raised, whitish rim; hymenium 150–190 μm; spores brown, muriform, 9–15 × 12–18 μm, 1–2 × 3–5 loculate, I–.

CHEMISTRY. Psoromic acid or no substances present.

HABITAT. Lianas and canopy branches in rain forest at lower elevations (150–350 m).

DISTRIBUTION. India, Sri Lanka, Philippines.

ADDITIONAL SPECIMEN. Hale collections: 5 (46 242) (no substances present), 6 (47 210), 7a (50 094), 7b (51 005, 51 016, 51 238), 8 (47 014) (no substances present).

OBSERVATIONS. The pore is often very deep, much as in *M. mastarion*, a related species. A. L. Smith made the combination in *Leptotrema* when identifying some collections from New Caledonia, but I have not been able to locate the specimen in BM for verification.

5. **Myriotrema cinereoglaucescens** (Vainio) Hale in *Mycotaxon* **11** : 132 (1980). (Fig. 11e)

Thelotrema cinereoglaucescens Vainio in *Suomal. Tiedeakat. Toim.* A. **15**(6) : 189 (1921). Type: Philippines, prov. Sorsogon, Irosin, Mt Bulusan, Nov. 1915, *Elmer* 14957 p.p. (TUR—lectotype; BM, FH, L, W—isolectotypes).
Ocellularia cinereoglaucescens (Vainio) Zahlbr., *Cat. Lich. Univers.* **2** : 586 (1923).

Thallus dull greenish gray, *c.* 10 cm diam, shiny, continuous; cortex dense, 10–20 μm, with abundant aculeate hyphae, splitting and exfoliating; algal layer continuous, 10–15 μm; medulla 20–30 μm with numerous crystals; apothecia abundant, immersed in the medulla, 0·3–0·5 mm diam, becoming slightly raised, exciple fused, colourless, columella lacking; pore round, about 0·1 mm diam; hymenium 45–50 μm; spores colourless, transversely septate, 4 × 10 μm, poorly developed, 5–6 loculate, I+.

CHEMISTRY. No substances present.

HABITAT. Lower trunk in rain forest at 100–200 m elevation.

DISTRIBUTION. Sri Lanka, Philippines, Hawaii.

ADDITIONAL SPECIMENS. Hale collections: 3a (46 363).

OBSERVATIONS. This is the first report of the species since the original description. It is probably close to *M. album* but the apothecia are always slightly raised. I did not find a columella, even in the type collection, contrary to Vainio's description. Vainio found spores 8–9 × 18–22 μm. The Hawaiian specimen (*Forbes* 2229 in US) has spores 18 μm long. The Sri Lankan material is obviously immature.

6. **Myriotrema compunctum** (Ach.) Hale in *Mycotaxon* **11** : 133 (1980). (Fig. 11f)

Urceolaria compuncta Ach., *Meth. Lich.*: 143 (1803). Type: Indonesia, Amboyna, *Christopher Smith* s.n. (LINN-Sm. 1692·7—lectotype; H-Nyl. 22447—isolectotype).
Leptotrema compunctum (Ach.) Müll. Arg. in *Flora, Jena* **71** : 527 (1888).
For additional synonymy see Salisbury, 1971*b* : 275.
ICONES. Salisbury, 1971*b* : 276 fig. 5 and 1978 : 416 fig. 10.

Thallus white, brownish, or turning dull red, 4–6 cm broad, dull, continuous; cortex lacking but a thin irregularly pored polysaccharide layer often present; medulla compact and cellular, to 150 μm, with algae located between vertical arrays, crystals abundant; apothecia immersed, 0·15–0·2 mm diam, the exciple apically free, colourless; disc pulling away from the wall, dark brown to white pruinose; pore round to irregular, 0·05–0·08 mm diam, partially filled with excipular material; hymenium 30–35 μm; spores brown, muriform, 8 × 10–16 μm, 1–2 × 4–6 loculate, I−.

CHEMISTRY. Norstictic acid and traces of stictic acid.

HABITAT. Trees at edge of scrub forest at low elevations.

DISTRIBUTION. United States, West Indies, Central and South America, Angola, Mozambique, Sri Lanka, Java, Philippines, Indonesia.

Additional specimens. Buttawa, Ruhuna National Park, *Fosberg et al.* 51 033 (US). Thwaites collections: C. L. s.n. (as 'Lgt. 85. *Thelotrema punctulatum*') (BM, S, UPS).

Observations. This is one of the best known species in the family, collected widely and usually correctly identified. It occurs in semi-arid forest and in disturbed areas which I did not visit in Sri Lanka. Leighton sent a specimen (C. L. 31 = *Thelotrema platysporum*) to Nylander, who called it '*T. punctulatum* Nyl. L. Exot. 222.' The remaining material, which Nylander did not see, is *M. compunctum*.

7. Myriotrema costaricense (Müll. Arg.) Hale in *Mycotaxon* **11** : 133 (1980).
(Fig. 11g)

Ocellularia costaricensis Müll. Arg. in *Bull. Soc. r. Bot. Belg.* **30** : 75 (1891). Type: Costa Rica, Baie de Sabines, 1890, *Pittier* s.n. (G—lectotype; US (as 5321), W—isolectotypes).
Ocellularia alba f. *costaricensis* (Müll. Arg.) Redinger in *Ark. Bot.* **28A**(8) : 45 (1936).
Rhabdodiscus costaricensis (Müll. Arg.) Vainio in *Suomal. Tiedeakat. Toim.* A, **15**(6): 184 (1921).

Thallus pale greenish to whitish gray, 8–15 cm broad, shiny, continuous or cracked at maturity; cortex dense, 15 μm thick, with aculeate hyphae, splitting and exfoliating; algal layer 10–15 μm; medulla to 100 μm with remnants of cortical layers and numerous crystals; apothecia common, semi-emergent, 0·4–0·7 mm diam, the exciple free apically; disc open, more or less fissured with superficial columella-like bridging; hymenium 55–60 μm; spores colourless, transversely septate, 4 × 10–15 μm, 5–6 loculate, I–.

Chemistry. Psoromic acid.

Habitat. Lower to mid trunk in rain forest at low elevations (150–300 m).

Distribution. Costa Rica, Sri lanka.

Additional specimens. Hale collections: 6 (47 199), 9 (46 137, 46 143).

Observations. Müller recognized the essential features of this species: raised apothecia, the wide pore with an essentially open disc, and the disc 'subreticulatis fenestratum'. The 'columellate' structures are not carbonized and for this reason Vainio was in error when he transferred it to *Rhabdodiscus*. The material from Sri Lanka matches the Costa Rican type well, but I would hardly claim that the species is well understood. Although Redinger recognized it as a variety of *Ocellularia (Myriotrema) alba*, that species lacks any lichen substances and has flush apothecia. Müller himself placed it near *Ocellularia viridi-alba* (Krempelh.) Müll. Arg. (= *Myriotrema viridi-album* (Krempelh.) Hale), but the type of *Thelotrema viridi-album* in M has muriform, colourless sproes, lichexanthone, and coarse isidia.

8. Myriotrema decorticatum Hale **sp. nov.**
(Fig. 11h)

Thallus corticola, pro parte hypophloeodes, albidus, nitidus, continuus, 6–10 cm latus; apothecia immersa, aetate pauce elevata, 0·2–0·4 mm diametro, excipulo connato apice pallide obfuscato; ostiolum rotundatum, nigro-cinctum, 0·05–0·1 mm diametro; hymenium 90–150 μm; sporae fuscae, murales, octonae, 6–12 × 18–24 μm, 1–3 × 5–7 loculate, I–.
Type: Sri Lanka, Matara District, Enselwatta, virgin mossy forest, 14 Feb. 1976, *M. E. Hale* 46 259 (US—holotypus; AMH, PDA—isotypi).

Thallus white to ashy gray, thin and in part hypophloeodal, shiny, continuous, 6–10 cm broad; cortex very thin, *c.* 5 μm, medulla variable, 10–100 μm; apothecia immersed in the medulla, slightly raised at maturity, 0·2–0·4 mm diam, often clustered, the exciple fused, turning brownish apically; pore round, dark rimmed, 0·05–0·1 mm diam; hymenium 90–150 μm; spores brown, muriform, 6–12 × 18–24 μm, 1–3 × 5–7 loculate, I–.

Chemistry. Stictic and constictic acid.

HABITAT. Lower bole to canopy of trees in virgin rain forest at 150–1000 m elevation.

DISTRIBUTION. Sri Lanka.

ADDITIONAL SPECIMENS. Hale collections: 3a (46 303), 6 (47 204).

OBSERVATIONS. The poorly developed cortex is a consistent character for this inconspicuous species. All other species of *Myriotrema* that I have seen have a well developed cortex. The closest relative is probably *M. fissurinum* (below), and I had in fact first identified it as that species.

9. **Myriotrema desquamans** (Müll. Arg.) Hale in *Mycotaxon* **11** : 133 (1980). (Fig. 11i)

Anthracothecium desquamans Müll. Arg. in *Flora, Jena* **71** : 48 (1888). Type: Australia, Johnstowns River, North Queensland, 1883, *F. v. Müller* s.n. (G—lectotype).

Thelotrema irosinum Vainio in *Suomal. Tiedeakat. Toim.* A, **15**(6) : 174 (1921). Type: Philippines, Prov. Sorsogon, Irosin, Oct. 1915, *Elmer* 14 749 (TUR—lectotype; FH, G, L, W—isolectotypes).

Leptotrema irosinum (Vainio) Zahlbr., *Cat. Lich. Univers.* **2** : 635 (1923).

Leptotrema desquamans (Müll. Arg.) Patw. & Makh. in *Bryologist* **83** : 368 (1980).

Thallus pale greenish mineral gray or straw coloured, 6–12 cm broad, shiny, continuous; cortex dense, 15–20 μm, with short aculeate hyphae, splitting and exfoliating; algal layer 10–15 μm, interrupted by crystals; medulla 30–50 μm, with dense crystals and remnants of cortical sheets; apothecia partially immersed in periderm, slightly emergent, concolorous with the thallus and inconspicuous, 0·3–0·4 mm diam, the exciple fused, reddish brown; pore very tiny, 0·05 mm diam, reddish or white rimmed; hymenium 140–160 μm; spores brown, muriform, 10–15 × 20–33 μm, 1–3 × 5–7 loculate, I−.

CHEMISTRY. Stictic and constictic acids.

HABITAT. Lianas, lower trunk, rarely in the canopy of trees in rain forest at low to mid elevations (150–850 m).

DISTRIBUTION. India, Sri Lanka, Philippines, Sabah, Australia.

ADDITIONAL SPECIMENS. Hale collection: 2 (51 162, 51 166, 51 223), 3a (46 335, 46 342, 46 349), 6 (47 207, 47 209), 7a (50 151, 50 154, 50 187), 7b (50 304, 51 049, 51 080), 8 (47 003, 47 006, 47 022, 47 026), 9 (46 163). Thwaites collections: C. I. 144 (BM, PDA, S, UPS), C. L. 281, 284 (PDA) (as 'Lgt. 86. *Thelotrema phaeosporum*'); C. L. 175 (UPS) (as 'Lgt. 87. *Thelotrema myriotrema*').

OBSERVATIONS. The tiny pore misled Müller to describe this species as an *Anthracothecium*. He did note that the thallus was 'plaguliformi-desquamans' and cross sections show considerable exfoliation. It is a member of a large, stictic acid-containing complex which includes *M. deceptum* (Hale) Hale, *M. phaeosporum* (Nyl.) Hale, *M. reclusum* (Krempelh.) Hale, and *M. trypaneoides* (Nyl.) Hale, all with a tiny pore and easily confused with non-carbonized pyrenocarpous genera. More distantly related are *M. elachistoteron* and *M. fissurinum* (see below) and *M. subcompunctum* (Nyl.) Hale. Nylander identified C. L. 144 as '*Thelotrema phaeosporum*', which differs in having immersed, flush apothecia. *Myriotrema desquamans* is distingushed by the semi-emergent apothecia and small spores. It is one of the most commonly collected species of *Myriotrema* in Sri Lanka.

10. **Myriotrema elachistoteron** (Leighton) Hale in *Mycotaxon* **11** : 133 (1980). (Fig. 12a)

Thelotrema elachistoteron Leighton in *Trans. Linn. Soc. Lond.* **27** : 169 (1870). Type: Sri Lanka, Central Province, *Thwaites* C. L. 132 (BM—lectotype).

Leptotrema elachistoteron (Leighton) Patw. & C. Kulk. in *Norw. J. Bot.* **24** : 128 (1977).

Thallus pale tannish gray, 3–5 cm broad, grainy to verruculose, continuous; cortex dense, 10–15 μm, bulging out above large crystals; algal layer 10–15 μm, interrupted by crystals; medulla to 30 μm, mostly hypophloeodal; apothecia numerous, immersed in the medulla, 0·25–0·3 mm diam, slightly raised at maturity, the exciple fused to partially free at the tips, colourless; pore 0·05–0·1 mm diam, sometimes darkened; hymenium 150–180 μm; spores brown, muriform, 25 × 80–90 μm, with numerous locules, 2–4/ascus, I–.

CHEMISTRY. Stictic and constictic acids.

HABITAT. Lower trunks in rain forest at lower elevations (300 m).

DISTRIBUTION. Sri Lanka.

ADDITIONAL SPECIMENS. Hale collections: 7a (50 170).

OBSERVATIONS. Although *M. elachistoteron* was described from Sri Lanka, it is very rare there; I collected it only once. Duplicates of the type collection ('Lgt. 92') are all mixtures of *M. fissurinum* (see below) and only the small collection in BM can be used for typification. Basically the most important characters are the medium to large spores and the non-exfoliating cortex with a somewhat grainy or finely verruculose surface. I believe that *Leptotrema microglaenoides* (Vainio) Zahlbr. is a synonym (see Hale, 1974*a* : 40) but would like to see more specimens from the New World. In my discussion of that species in Dominica I mentioned that *Leptotrema (Thelotrema) monosporum* had stictic acid. This determination was based on a specimen identified by Nylander in PC, but it is not part of the type collection. *Thelotrema monosporum* (see above) lacks lichen substances. Salisbury (1975 : 61) adds *Leptotrema subgeminum* (Nyl.) Zahlbr. as a synonym but I would hesitate to confirm this on the basis of the very poor fragment in H-Nyl., even though the chemistry and spores are similar.

11. **Myriotrema eminens** (Hale) Hale in *Mycotaxon* **11** : 133 (1980).
(Fig. 12b)

Thelotrema eminens Hale in *Mycotaxon* **3** : 177 (1975). Type: Malaya, Pahang, Gunong Brinchang, 3 Mar. 1965, *M. E. Hale* 29 947 (US—holotype).
ICONES. Hale, 1975 : 181 fig. 9.

Thallus pale ashy green, 6–10 cm broad, shiny, fissured, sometimes coarsely isidate; cortex very thin, 5 μm, with aculeate hyphae; algal layer continuous, 10–15 μm; medulla 30–60 μm with numerous crystals; apothecia clumped, emergent to urceolate, 0·4–0·5 mm diam, the exciple free apically, reddish brown, often visible through and partially filling the pore; pore round, 0·1–0·15 mm diam; hymenium 190–200 μm; spores colourless, muriform, 20–30 × 120–150 μm, with numerous locules, 2–4/ascus, I+.

CHEMISTRY. Stictic acid, probably with traces of norstictic acid.

HABITAT. Canopy of trees in rain forest at lower elevations (150–350 m).

DISTRIBUTION. Sri Lanka, Malaya, Philippines.

ADDITIONAL SPECIMENS. Hale collections: 4 (47 058, 47 140), 6 (47 183), 9 (46 202).

OBSERVATIONS. The apothecia are distinctly urceolate at maturity, although at earlier stages they are not strongly emergent. They also tend to occur in distinct clusters 1 cm or more across.

12. **Myriotrema fissurinum** Hale **sp. nov.**
(Fig. 12c)

Thallus corticola, epiphloeodes, viridi-albicans, nitidus, aetate fissurinus, 7–12 cm latus; apothecia immersa, pro parte aggregata, 0·2–0·25 mm diametro, excipulo apice libero, columella nulla; ostiolum 0·05 mm diametro; hymenium 70–150 μm altum; sporae fuscae, murales, 10–12 × 27–32 μm, 0–2 × 4–7 loculate, 4–8/ascus, I–.

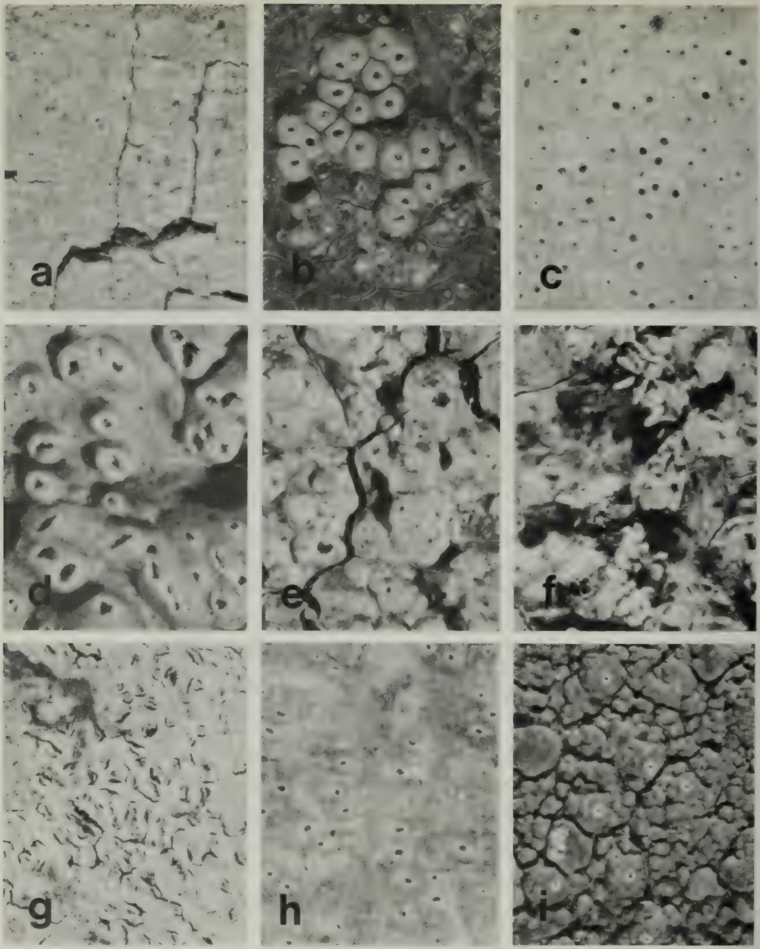

Fig. 12 Species of *Myriotrema*. (a) *M. elachistoteron* (Hale 50 170). (b) *M. eminens* (Hale 47 183). (c) *M. fissurinum* (Hale 46 227). (d) *M. fluorescens* (Hale 46 244). (e) *M. frondosum* (apothecia) (Hale 51 232). (f) *M. frondosum* (isidia) (Hale 51 232). (g) *M. glaucescens* (Hale 50 334). (h) *M. glaucophaenum* (Hale 47 148). (i) *M. granulosum* (Hale 47 092). See Fig. 7i for scale.

Typus: Sri Lanka, Southern Province, Matara District, mossy forest above Enselwatta, elev. 1100 m, 14 Feb. 1976, *M. E. Hale* 46 227 (US—holotypus; BM—isotypus).

Thallus whitish to pale greenish gray or tan, 7–12 cm broad, shiny, smooth, fissured with age; cortex dense, 8–12 μm; algal layer continuous, 10–15 μm; medulla to 100 μm, with crystals; apothecia immersed in the medulla, often in masses, 0·2–0·25 mm diam, the exciple free at the tips, pale yellowish brown, partially filling the pore; pore nearly closed and darkening to open, 0·05 mm diam; hymenium 70–150 μm; spores brown, muriform, 10–12 × 27–32 μm, 1–2 × 4–7 loculate, 4–8/ascus, I−.

CHEMISTRY. Stictic and constictic acids.

HABITAT. Branches and lower trunk of trees in rain forest at mid and higher elevations (1100–2100 m).

DISTRIBUTION. India, Sri Lanka.

ADDITIONAL SPECIMENS. Hale collections: 5 (46 221), 1 (50 331). Thwaites collections: C. L. 120, 122 (BM, H-Nyl. 3885, 3886, PDA, S, UPS) (as 'Lgt. 82. *Thelotrema glaucopallens*'), C. L. 12 (BM, H-Nyl. 3874, PDA, S, UPS), C. L. (BM, PDA) (as 'Lgt. 83. *Thelotrema compunctum* Sm.'). India: Tamil Nadu, 3 km S Naduvattam, *Hale* 50 835, 50 844, 50 845, (US); Kerala, Devicolam, *Hale* 46 568 (US), Munnar, *Hale* 47 344, 47 355 (US).

OBSERVATIONS. This species is closely related to *M. subcompunctum* (Nyl.) Hale, which I reported erroneously from Dominica (Hale, 1974*a* : 42). After more critical examination of type material in PC, I would now delimit *M. subcompunctum* as having a dull, weakly organized and porous cortex about 20 μm thick, a medulla to 150 μm thick arranged in vertical blocks with large crystalline inclusions, and spores 15–17 μm long. I have also discovered two synonyms, *Leptotrema diffractum* Müll. Arg. from Australia (type: *Bailey* in G) and *L. inclusum* Zahlbr. from Japan (type: *Faurie* 5147 in W). Very close and perhaps representing additional synonyms are *L. polycarpum* Müll. Arg. from Australia (type: *Knight* in G) and *L. polyporum* Riddle from the West Indies (type: *Jennings* 229a in FH). I have not yet redetermined the Dominican collection.

The material which I am describing here as *M. fissurinum* differs subtly but significantly in having a shiny, dense cortex 15 μm thick, a thick, continuous algal layer, and a medulla 60–120 μm thick with small grainy crystals, not organized in vertical arrays. The spores are also consistently larger than in *M. subcompunctum*, 21–32 μm long. It is now known from southern India and Sri Lanka, generally above 1000 m elevation.

Leighton had Nylander confirm the identification of '*T. glaucopallens*'. Notwithstanding, *Thelotrema glaucopallens* Nyl. (see Hale, 1978*a* : 43 and Salisbury, 1971*b* : 274) has colourless spores and an exfoliating cortex. While quite common in neighbouring India, I did not collect the species in Sri Lanka. Leighton also misidentified C. L. 12 and C. L. 129 as '*T. compunctum* Sm.', which does occur in Sri Lanka but is not related at all to *M. fissurinum*.

13. Myriotrema fluorescens Hale sp. nov.

(Fig. 12d)

Thallus corticola, epiphloeodes, nitidus, continuus, 6–20 cm latus; apothecia immersa, rotundata sed aetate elongata, 0·5–1·0 mm diametro, margine thallino suberecto, excipulo libero; ostiolum rotundatum vel elongato-fissum, 0·2–0·5 mm lato; hymenium 45–65 μm altum; sporae incolores, murales 4–8 × 12–15 μm, 1–2 × 4 loculatae, I+ coeruleae.

Typus: Sri Lanka, Southern Province, Matara District, mossy forest above Enselwatta, elev. 1100 m, 14 Feb. 1976, *M. E. Hale* 46 244 (US—holotypus; BM—isotypus).

Thallus greenish mineral gray, 6–20 cm broad, shiny, continuous; cortex dense, 30–40 μm, with aculeate hyphae, splitting into numerous sheets; algal layer continuous, 15 μm; medulla 150–250 μm with incorporated cortical sheets; apothecia immersed to semi-emergent, often in lirelliform-like clusters, the thalline rim suberect, apically crumbling with age and almost sorediate, exciple free apically, pale reddish brown, partially filling the pore;

pore gaping, round to slit, 0·2–0·5 mm wide; hymenium 45–65 μm; spores colourless, muriform, 4–8 × 12–15 μm, 1–2 × 4 loculate, I+.

CHEMISTRY. Lichexanthone.

HABITAT. Lower trunks of trees at low to mid elevations (300–1100 m).

DISTRIBUTION. Sri Lanka.

ADDITIONAL SPECIMENS. Hale collections: 1 (50 211, 50 218), 2 (51 124, 51 144, 51 170), 4 (47 152). Thwaites collections: Lgt. 192 (BM, S) (as 'Lgt. 192. *Trypethelium schizostomum*').

OBSERVATIONS. The elongate apothecia, thick, exfoliating cortex, and presence of lichexanthone mark this as an extraordinary species. It may be one of the possible bridges to the Graphidaceae, although the excipular structure is thelotremoid.

When Thwaites divided the material of C. L. 121 (*Trypethelium schizostomum*), the Leighton set included only the species which I have determined as *Ocellularia fissa* (see below). Duplicates in BM and S are *M. fluorescens.*

14. **Myriotrema frondosum** Hale **sp. nov.**

(Fig. 12e, f)

Thallus corticola, epiphloeodes, viridi-albus, 4–6 cm latu, crasse isidiatus, isidiis squamuloso-divisis; apothecia immersa, *c.* 0·2 mm diametro, excipulo libero, incolorato, columella nulla; ostiolum rotundatum, 0·05 mm diametro; hymenium 115–125 μm altum; sproae incolores, murales, octonae, 9–10 × 21–24 μm, 1–2 × 5–6 loculatae, I+ coeruleae.

Typus: Sri Lanka, Sabaragamuwa Province, Ratnapura District, Halwathura-Kanda, near Rassagala, elev. 900 m 15 Mar. 1978, *M. E. Hale* 51 232 (US—holotypus).

Thallus light greenish gray, 4–6 cm broad, shiny, deeply fissured, coarsely isidiate, the isidia turning into flattened squamule-like excrescences 1 mm wide and 1–1·5 mm high; cortex dense, 10–12 μm, with aculeate hyphae, splitting somewhat; algal layer 15 μm; medulla 30–50 μm; apothecia sparse and inconspicuous, immersed in the medulla, 0·2 mm diam, the exciple colourless, free apically, in part filling the pore; pore round, 0·05 mm diam; hymenium 115–125 μm; spores colourless, muriform, 9–10 × 21–24 μm, 1–2 × 5–6 loculate, I+.

CHEMISTRY. Psoromic acid.

HABITAT. Tree trunks at mid elevations in mossy forest (900 m).

DISTRIBUTION. Sri Lanka.

OBSERVATIONS. This species produces clumps of unique, isidioid, subfoliar structures. I first thought that I had collected a *Myriotrema* species overgrowing a liverwort, but the growths are entirely lichenized. It is a member of the '*Thelotrema album*' group.

15. **Myriotrema glaucescens** (Nyl.) Hale in *Mycotaxon* **11** : 133 (1980).

(Fig. 12 g)

Thelotrema glaucescens Nyl. in *Annls Sci. nat.* (Bot.) IV, **19** : 332 (1863). Type: USA, Louisiana, *Dr Hale* s.n. (FH-Tuck.—lectotype).

Leptotrema glaucescens (Nyl.) Müll. Arg. in *Flora, Jena* **65** : 499(1882).

ICONES. Redinger, 1936 : 108 fig. 68.

Thallus whitish mineral gray, 3–10 cm broad, dull, fissuring and sometimes bulging out; cortex lacking; medulla compact, cellular, 150–200 μm with algae between vertical blocks; apothecia immersed in the medulla, round to angular, 0·2–0·3 mm long, often massed, the exciple fused, the disc pulling away from the wall; disc blackish to white pruinose; hymenium 90–130 μm; spores brown, muriform, 7–10 × 13–16 μm, 1–2 × 4 loculate, uniseriate, I—.

CHEMISTRY. Stictic and constictic acids.

HABITAT. Planted trees at mid or higher elevations (500–2100 m).

DISTRIBUTION. United States, West Indies, Central and South America, India, Sri Lanka.

ADDITIONAL SPECIMENS. Hale collections: 11 (50 334), 13 (50 049). Thwaites collections: C. L. 119 (BM, H-Nyl. 3918, S, UPS) (as 'Lgt. 74. *Th. glaucescens*'). Alutnuwara, *Alston* 1952 (PDA).

OBSERVATIONS. This species can be recognized easily by the crowded, black, angular apothecia and the presence of stictic acid. The thallus surface is dull and grainy since medullary hyphae are exposed directly (Fig. 5a). Leighton correctly identified it by comparison with Wright's Lich. Cubae 151 and 152.

16. **Myriotrema glaucophaenum** (Krempelh.) Hale in *Mycotaxon* **11** : 133 (1980). (Fig. 12h)

Thelotrema glaucophaenum Krempelh. in *Nuovo G. bot. ital.* 7 : 19 (1875). Type: Sarawak, 1866, *Beccari* 92 (M—lectotype; G—isolectotype).
Ocellularia glaucophaena (Krempelh.) Zahlbr., *Cat. Lich. Univers.* **2** : 591 (1923).
ICONES. Hale, 1978*a* : 5, 22 fig. 1r (lectotype) and fig. 6b.

Thallus pale greenish to yellowish mineral gray, 8–10 cm broad, shiny, continuous; cortex dense, 10–15 μm, with aculeate hyphae, splitting internally with some exfoliation; algal layer continuous, 10–12 μm; medulla 10–90 μm with crystals; apothecia barely emergent, 0·3–0·4 mm diam, the exciple fused, colourless, columella lacking; pore round, 0·1–0·15 mm diam; hymenium *c.* 60 μm; spores colourless, transversely septate, 3–5 × 6–12 μm, 3–4 loculate, I+.

CHEMISTRY. Psoromic acid.

HABITAT. Lower trunk and lianas in rain forest at low elevations (250–350 m).

DISTRIBUTION. United States, West Indies, Central America, India, Sri Lanka, Java, Sarawak, Solomon Islands.

ADDITIONAL SPECIMENS. Hale collections: 4 (47 059, 47 061, 47 062, 47 148), 7b (51 247).

OBSERVATIONS. The material from Sri lanka is very close to the type specimen in all respects. It can be usually be distinguished from *M. terebratulum* by the raised apothecia and thinner thallus. This complex, however, is a difficult one and the species limits are unsettled (see Hale, 1978*a* : 21).

17. **Myriotrema granulosum** (Leighton) Hale in *Mycotaxon* **11** : 133 (1980). (Fig. 12i)

Ascidium granulosum Leighton in *Trans. Linn. Soc. Lond.* **27** : 171 (1870). [Non *Ocellularia granulosa* (Tuck.) Zahlbr. ex anno 1923]. Type: Sri Lanka, south of the island, *Thwaites* C. L. 127 (BM—lectotype; G, PC—isotectotypes).
Ocellularia leightonii Zahlbr., *Cat. Lich Univers.* **2** : 593 (1923). Based on *Ascidium granulosum.*

Thallus greenish mineral gray, 7–12 cm broad, coarsely verrucose and deeply fissured; cortex dense, 10–12 μm; algal layer continuous, 12 μm; medulla 15 μm, pale yellowish, mostly hypophloeodal; apothecia numerous, emergent, 0·3–0·5 mm diam, slightly constricted basally and appearing urceolate at maturity, the exciple fused, reddish brown, free apically, columella lacking; pore round, 0·05 mm diam, distinctly white annulate; hymenium 280–300 μm; spores colourless, transversely septate, 15–18 × 90–150 μm, 14–16 loculate, rarely with a longitudinal septum in the end loculae, 1–2/ascus, I+.

CHEMISTRY. Unknown P+ substance ('leightonii' unknown).

HABITAT. Saplings, mid bole and canopy in rain forest at lower elevations (200–300 m).

DISTRIBUTION. Sri Lanka.

ADDITIONAL SPECIMENS. Hale collections: 4 (47 060, 47 092, 50 487, 50 512), 6 (47 173, 47 187), 7a (50 152). Thwaites collections: C. L. 127 (BM, G, H-Nyl. 3870, PC) (as 'Lgt. 100, *Ascidium granulosum*', C. L. 260 (PDA).

OBSERVATIONS. This endemic species is remarkable for the almost urceolate apothecia, coarsely verruculose thallus, large spores, and the unique chemistry and pale yellow medullary pigment. The P+ unknown substances is probably an undescribed depsidone.

18. Myriotrema hartii (Müll. Arg.) Hale in *Mycotaxon* **11** : 133 (1980).
(Fig. 13a, b)

Thelotrema hartii Müll Arg. in *Flora, Jena* **69** : 311 (1886). Type: Jamaica, Gordontown, *Hart* s.n. (G—lectotype; BM, NY (as no. 36)—isolectotypes).

Thallus pale greenish white, *c.* 8 cm diam, shiny, deeply fissured, coarsely isidiate, the isidia 0·2 mm diam and to 0·8 mm high; cortex dense and irregularly thickened, 8–15 μm, with aculeate hyphae; algal layer continuous, 15–20 μm; medulla 10–60 μm with crystals; apothecia numerous, immersed in the medulla, 0·2–0·3 mm diam, the thalline rim becoming raised with age, exciple apically free, pale yellowish, visible through the pore, columella lacking; pore round, 0·1–0·15 mm diam, white rimmed; hymenium *c.* 40 μm; spores colourless, muriform, 6 × 13–15 μm, 1–2 × 4 loculate, I+.

CHEMISTRY. Psoromic acid.

HABITAT. Branches in open forest at high elevations (2100 m).

DISTRIBUTION. West Indies, Central and South America, Sri Lanka.

ADDITIONAL SPECIMENS. Hale collections: 10 (50 270).

OBSERVATIONS. When describing *Thelotrema hartii,* Müller Argoviensis did not mention any 'isidia', although these structures are quite distinct and present in the type material. It is indeed very close to *M. concretum* (Fée) Hale, as he suggested, and may prove eventually to be merely a morphological variant. One often collects coarsely isidiate but sterile thalli in the tropics closely resembling *M. hartii.* Since *M. hartii* often has very sparsely developed apothecia, it may well be widely distributed as these sterile crusts.

19. Myriotrema masonhalei (Patw. & C. Kulk.) Hale in *Mycotaxon* **11** : 134 (1980).
(Fig. 13c)

Thelotrema masonhalei Patw. & C. Kulk. in *Norw. J. Bot.* **24** : 128 (1977). Type: India, Maharashtra, Amboli, *A. V. Prabhu & M. B. Nagarkar* 74.2262 (AMH—holotype).
ICONES. Patwardhan & Kulkarni, 1977 : 129 fig. 4.

Thallus whitish ashy gray, 6–12 cm broad, shiny, smooth to verruculose, fissured with age; cortex dense, irregularly thickened, 8–15 μm, with some aculeate hyphae; algal layer continuous, 10 μm; medulla 0–60 μm with crystals, mostly hypophloeodal; apothecia inconspicuous, immersed deeply in the periderm, 0·5–0·7 mm diam, exciple fused, colourless, columella lacking; pore round, 0·05–0·08 mm diam, white rimmed; hymenium 180–350 μm; spores colourless, muriform, 30–45 × 150–250 μm, with numerous locules, 1/ascus, I+.

CHEMISTRY. Psoromic acid.

HABITAT. Lianas, saplings, and exposed roots, rarely into the canopy, in rain forest over broad elevations (150–2100 m).

DISTRIBUTION. India, Sri Lanka.

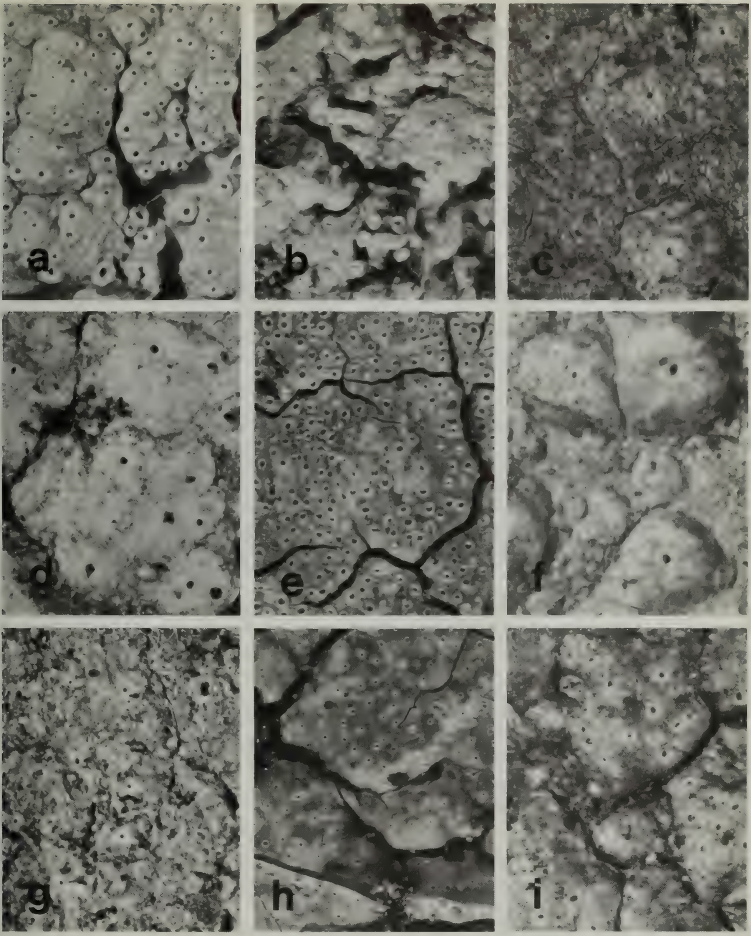

Fig. 13 Species of *Myriotrema*. (a) *M. hartii* (apothecia) (Hale 50 270). (b) *M. hartii* (isidia) (Hale 50 270). (c) *M. masonhalei* (Hale 46 341). (d) *M. mastarion* (Hale 51 039). (e) *M. microporum* (Hale 46 217). (f) *M. microstomum* (Hale 46 223). (g) *M. minutulum* (Hale 46 358). (h) *M. minutum* (Hale 47 033). (i) *M. multicavum* (Hale 46 150). See Fig 7i for scale.

ADDITIONAL SPECIMENS. Hale collections: 1 (50 214, 50 219, 50 252 50 260), 2 (51 164), 3a (46 290, 46 341, 46 347, 46 348), 4 (47 071, 47 111, 47 128, 50 382), 6 (47 196), 7a (50 178), 7b (51 024, 51 082, 51 250), 8 (47 027), 9 (46 215), 10 (50 264, 50 288).

OBSERVATIONS. This is the third most common *Myriotrema* in Sri Lanka. It is also common in the evergreen monsoon forests of the Western Ghats in India. The deeply immersed apothecia are very inconspicuous, their presence indicated only by the tiny, white rimmed pore. However, once the large spores are found and the chemistry determined, the species is easily identified.

20. **Myriotrema mastarion** Hale **sp. nov.**

(Fig. 13d)

Thallus corticola, epiphloeodes, nitidus, continuus, 8–10 cm latus; apothecia profunde immersa, 0·3–0·4 mm diametro, excipulo connato, columella nulla; ostiolum rotundatum, 0·08–0·1 mm diametro; hymenium 120–180 μm altum; sporae fuscae, octonae, transversim septatae, 5–9 × 15–21 μm, 4 loculatae, I–.

Typus: Sri Lanka, Western Province, Kalatura District, Morapitiya, Ambalam-pola, elev. 300 m, 13 Mar. 1978, *M. E. Hale* 51 039 (US—holotypus; BM—isotypus).

Thallus ashy greenish or tannish gray, 8–10 cm broad, shiny, continuous, faintly grainy; cortex loosely organized and irregularly pored, 12 μm; algal layer 10–20 μm, more or less interrupted by crystals; medulla 15–45 μm, sometimes faintly yellowish, with crystals; apothecia inconspicuous, deeply immersed in periderm layers, 0·3–0·4 mm diam, the exciple fused, reddish brown, columella lacking; pore round, 0·08–0·1 mm diam, the rim raised, tannish white; hymenium 120–180 μm; spores brown, inconspicuous, deeply immersed in periderm layers, 0·3–0·4 mm diam, the exciple fused, reddish brown, columella lacking; pore round, 0·08–0·1 mm diam, the rim raised, tannish white; hymenium 120–180 μm; spores brown, transversely septate, 5–9 × 15–21 μm, 4 loculate, I—.

CHEMISTRY. Psoromic and norpsoromic acids.

HABITAT. Trunks along open trails and in canopy in rain forest at low to mid elevations (150–850 m).

DISTRIBUTION. Sri Lanka.

ADDITIONAL SPECIMENS. Hale collections: 2 (51 233), 4 (47 159, 50 520), 9 (46 207).

OBSERVATIONS. This species closely resembles *M. andamanicum* (see above) in apothecial structure and chemistry; only the spores are different (muriform in *M. andamanicum*).

21. **Myriotrema microporum** (Mont.) Hale in *Mycotaxon* **11** : 134 (1980).

(Fig. 13e)

Thelotrema microporum Mont. in *Annls Sci. nat.* (Bot.) III, **10** : 130 (1848). Type: Java, *Junghuhn*, Lichen. Javan. 143 (PC—lectotype; FH-Tuck., G, H-Nyl., L—isolectotypes).
Thelotrema crassulum Nyl. in *Annls Sci. nat.* (Bot.) IV, **11** : 258 (1859). Type: Bourbon [= Réunion], *Biovin* s.n. (PC—lectotype; G, H-Nyl. 22652—isolectotypes).
Ocellularia micropora (Mont.) Müll. Arg. in *Flora, Jena* **74** : 112 (1891).
Ocellularia crassula (Nyl.) Zahlbr., *Cat. Lich. Univers.* **2** : 588 (1923).

Thallus light greenish to whitish mineral gray, 8–15 cm broad, thick and deeply fissured, smooth, shiny; cortex barely formed, about 5 μm, with aculeate hyphae; medulla densely cellular, columnar, 200–300 μm thick, the algae between vertical arrays in layers 10–25 μm; apothecia numerous, immersed in the medulla, 0·2–0·3 mm diam, the exciple more or less free apically, pale reddish, visible through the pore, columella lacking; pore round, 0·07–0·1 mm diam with a slightly raised whitish rim; hymenium 55–60 μm; spores colourless, transversely septate, 4 × 8–11 μm, 3–4 loculate, I+.

CHEMISTRY. Psoromic and norpsoromic acid.

HABITAT. Canopy branches in rain forest at mid higher elevations (300–2000 m).

DISTRIBUTION. Mascarene Islands, India, Sri Lanka, Malaya, Philippines, Java, Sabah, Taiwan, Japan, Solomon Islands, Australia.

ADDITIONAL SPECIMENS. Hale collections: 4 (47 083), 5 (46 271), 10 (50 287). Thwaites collections: C. L. 142 (PDA), C. L. 143 (BM, H-Nyl. 3852, S, UPS) (as 'Lgt. 75, *T. leptoporum*') (material in BM and S admixed with *Myriotrema olivaceum*).

OBSERVATIONS. Salisbury (1978 : 411) followed Redinger (1936 : 48) in considering this species as a synonym of *Thelotrema (Myriotrema) olivaceum*. As far as I can determine, these two species are not closely related, differing in both chemistry and morphology. *Myriotrema olivaceum* has a discrete, thick cortex (15–18 μm) and on average a thinner medulla (180–200 μm) than *M. microporum*. Nylander suggested that his *Thelotrema crassulum* might be combined *T. microporum* (he had undoubtedly seen the Montagne type in PC) and later (1869 : 70) questioned whether *T. microporum* was distinct from *Myriotrema album*. As I have shown above, *M. album* lacks any chemistry and has a much thinner thallus. The deep fissuring characteristic of *M. microporum* was first noted by Harmand (1912 : 36) as one way to separate it from *M. album*.

As far as the Sri Lankan flora is concerned. *M. microporum* might be confused with *M. terebratulum*, which has identical chemistry but a much thicker cortex (about 30 μm) and little fissuring. I have not yet identified *M. microporum* from the New World.

Leighton's determinations of '*Thelotrema microporum*', none of them checked by Nylander, are all incorrect. Some of the material is *M. thwaitesii* (see below), some *M. rugiferum* (below). At the same time he misidentified *M. microporum* as '*Thelotrema leptoporum* Nyl. = Wright's Lich. Cubae, 128!'. *Thelotrema leptoporum* Nyl. (see Hale, 1978*a* : 23) is a New World species with hypoprotocetraric acid and lichexanthone, a synonym of *Myriotrema glauculum* (Nyl.) Hale.

22. Myriotrema microstomum (Müll. Arg.) Hale in *Mycotaxon* **11** : 134 (1980).
(Fig. 13f)

Thelotrema microstomum Müll. Arg. in *Flora, Jena* **74** : 113 (1891). Type: Japan, Mt. Tosa, *Miyoshi* (G—lectotype; FH, TI—isolectotypes).

Thelotrema microstomum var. *formosanum* Zahlbr. in *Reprium Spec. nov. Regni veg.* **33:** 24 (1933). Type: Taiwan, Regechi, *Asahina* 233 (W—lectotype).

Thallus pale greenish ashy, 8–12 cm broad, shiny, irregularly cracked with age; cortex dense, 10–15 μm, with aculeate hyphae, splitting internally; algal layer continuous, 10–15 μm; medulla 5–20 μm with large crystals; apothecia rather numerous, emergent, solitary or clustered in 2's and 3's, 1–1·8 mm diam, the exciple fused, colourless; columella lacking; pore round, 0·1–0·18 mm diam, somewhat depressed, white rimmed and with white markings radiating outward over the amphithecium; hymenium 160–320 μm; spores colourless, muriform, 30–45 × 120–150 μm, with numerous locules, 1/ascus, I+.

CHEMISTRY. Fumarprotocetraric acid with traces of protocetraric acid.

HABITAT. Lower trunks of trees in mid elevation mossy forest (850–1100 m).

DISTRIBUTION. Japan, Taiwan, Sri Lanka.

ADDITIONAL SPECIMENS. Hale collections: 2 (51 098, 51 126, 51 137, 51 214), 5 (46 223, 46 228, 46 231, 46 236, 46 258, 46 261). Thwaites collections: C. L. 97 (BM), C. L. 257 (PDA) (mixed with *Ocellularia pertusariiformis*), Lgt. 96 (BM) (as '*T. pertusariiforme*').

OBSERVATIONS. The Sri Lankan material is very close to the Japanese type (it is identical to var. *formosanum*) in pore configuration, although the rim around the pore is not distinctly raised. The species is unusual because of the large, noncarbonized apothecia, large spores, and chemistry. Related *M. cinereum* (Müll. Arg.) Hale from Japan has fumarprotocetraric acid, but the apothecia are smaller and less emergent. Another species producing fumarprotocetraric acid, *M. secernendum* (Harm.) Hale, from New Caledonia has immersed apothecia and small spores (26 μm long).

23. **Myriotrema minutulum** (Hale) Hale in *Mycotaxon* **11** : 134 (1980).
(Fig. 13g)

Ocellularia minutula Hale in *Smithson. Contr. Bot.* **38** : 24 (1978). Type: Panama, Canal Zone, 11 Feb. 1974, *M. E. Hale* 43 341 (US—holotype).
Icones. Hale, 1978*a* : 22 fig. 6h.

Thallus pale greenish ashy, 8–12 cm broad, shiny, continuous, smooth to rugulose; cortex dense, 10–12 μm, with sparse aculeate hyphae; algal layer continuous, 6–10 μm; medulla 8–12 μm with numerous crystals, mostly hypophloeodal; apothecia common but not conspicuous, immersed deeply in periderm tissue, 0·2–0·3 mm diam, the exciple fused, colourless; pore round, 0·05–0·07 mm diam, slightly depressed and white rimmed; hymenium 80–100 μm; spores colourless, transversely septate, 5–6 × 15–24 μm, 5–6 loculate, I+.

Chemistry. Psoromic acid.

Habitat. Lower trunk to mid bole in rain forest at low elevations (300 m).

Distribution. Central America, Sri Lanka.

Additional specimens. Hale collections: 3a (46 358, 46 369), 7b (51 086, 51 093).

Observations. The apothecia are deeply immersed and inconspicuous. The species is probably related to *M. masonhalei*, which has larger apothecia and muriform spores.

24. **Myriotrema minutum** (Hale) Hale in *Mycotaxon* **11** : 134 (1980).
(Fig. 13h)

Ocellularia minuta Hale in *Mycotaxon* **7** : 379 (1978). Type: Sri Lanka, Southern Province, Morawaka Hill, 15 Feb. 1976, *M. E. Hale* 47 033 (US—holotype; BM, PDA—isotypes).
Icones. Hale, 1978*b* : 384 fig. 4.

Thallus greenish gray, 8–10 cm broad, thick, shiny, broadly fissured; cortex dense, 10–15 μm, with aculeate hyphae, splitting internally; algal layer continuous, 10–15 μm; medulla 150 μm or more with incorporated cortical sheets and dense crystal masses; apothecia very numerous, immersed in the medulla, 0·1–0·2 mm diam, the exciple fused, colourless; pore round, 0·05 mm diam, white rimmed; hymenium 60–70 μm; spores colourless, transversely septate, 4–6 × 18–20 μm, 4–5 loculate, I+.

Chemistry. Fumarprotocetraric acid.

Habitat. Lower trunks in rain forest at lower elevations (300–800 m).

Distribution. Sri Lanka, Sarawak.

Additional specimens. Hale collections: 2 (51116), 7a (50 315). Sarawak: Mt Matang, *Hale* 30 768 (US).

Observations. This is one of the few species in the genus with fumarprotocetraric acid. Other diagnostic features are the very small immersed apothecia and the thick, internally splitting cortex which is successively incorporated in the medulla as new tissue forms.

25. **Myriotrema multicavum** Hale **sp. nov.**
(Fig. 13i)

Thallus corticola, epiphloeodes, crassus, fere tumulatus, fissurinus, friabilis, cinereo-albus vel pallide viridis, 8–12 cm latus; apothecia numerosa, solitaria, profunde immersa, 0·2–0·3 mm diametro, excipulo apice libero, columella nulla; ostiolum rotundatum, *c.* 0·1 mm diametro; hymenium 100–120 μm altum; sporae incolorae, transversim septatae, octonae, male evolutae, 4 × 8 μm, 3–4 loculate, I+ coeruleae.

Typus: Sri Lanka, Southern Province, Galle District, Kanneliya Forest Reserve, elev. 150 m, 16 Feb. 1976, *M. E. Hale* 46 150 (US—holotypus; BM—isotypus).

Thallus pale greenish ashy, 8–12 cm broad, shiny, grainy, thick and deeply fissured, friable; cortex very thin, *c.* 5 μm and sometimes not distinguishable from the medulla, with long aculeate hyphae; medulla densely cellular, 200–300 μm thick in vertically oriented arrays, with dense crystals, the algae lying between columns; apothecia numerous, immersed in the medulla, 0·2–0·3 mm diam, the exciple free at the tips, colourless, visible through the pore; pore round, 0·1 mm diam; hymenium 100–120 μm; spores colourless, transversely septate, 4 × 8 μm, 3–5 loculate, poorly developed, I+.

Chemistry. Psoromic acid.

Habitat. Canopy of trees in rain forest at lower elevations (150–300 m).

Distribution. Sri Lanka.

Additional specimens. Hale collections: 4 (47 147).

Observations. This new species appears superficially to be close to *M. microporum* or *M. terebratulum*, but it can be separated by the grainy surface and the columnar, crystal-filled medulla (Fig. 5c).

26. Myriotrema nuwarense Hale sp. nov.

(Fig. 14a)

Thallus corticola, epiphloeodes, albo-cinereus, rimosus, usque ad 12 cm latus; apothecia immersa vel pauce emergentia, 0·2–0· mm diametro, excipulo libero, crasso, incolorato, columella nulla; ostiolum rotundatum, 0·1 mm diam; hymenium 200–210 μm altum; sporae fuscae, murales, octonae, 12–14 × 45–60 μm, 1–2 × 7–9 loculatae, 2 : nae, I–.

Typus: Sri Lanka, Central Province, Nuwara Eliya District, Forest Reserve near Nuwara Eliya, elev. 2100 m, 21 Mar. 1978, *M. E. Hale* 50 272 (US—holotypus; BM—isotypus).

Thallus whitish to tannish gray, to 12 cm broad, dull, fissured; cortex dense, 10–15 μm; algal layer continuous, 15–18 μm; medulla 60–120 μm, with some crystals; apothecia numerous, immersed in the medulla, slightly raised at maturity, 0·2–0·3 mm diam, exciple free apically, thickened, colourless, partially filling the pore; pore round, *c.* 0·1 mm diam; hymenium 200–210 μm; spores brown, muriform, 12–14 × 45–60 μm, 1–3 × 7–9 loculate, 2–4/ascus, I–.

Chemistry. Stictic and constictic acids.

Habitat. Small branches of trees at high elevations (2100 m).

Distribution. Sri Lanka.

Observations. It is with great hesitation that I describe another stictic acid-containing species of *Myriotrema*. However, *M. nuwarense* differs fairly strongly from others in the group in having immersed but conspicuous apothecia with an apically free exciple which fills the pore in part. The closest relative is probably *M. fissurinum* (see above).

27. Myriotrema olivaceum Fée, *Essai Crypt* : 103 (1824).

(Fig. 14b)

Type: ?South America, on *Bonplandia trifoliata* (G—lectotype; M, PC-Mont.—isolectotypes).
Ocellularia olivacea (Fée) Müll. Arg. in *Mém. Soc. Phys. Hist. nat. Genève* **29**(8) : 7 (1887).
Icones. Redinger, 1936 : 48 fig. 24.—Hale, 1974*a* : 7, 23 figs 5c and 12c (lectotype).—Hale, 1978*a* : 22 fig. 61.—Salisbury, 1978 : 410 fig. 4.

Thallus pale greenish ashy gray, 10–15 cm diam, smooth, shiny, continuous to fissured with

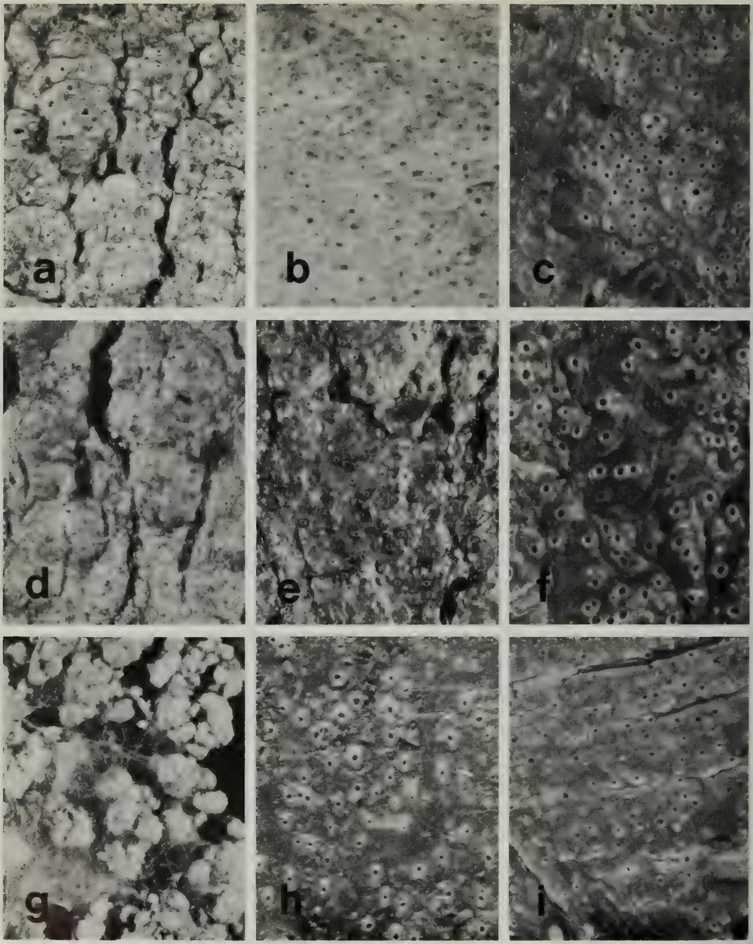

Fig. 14 Species of *Myriotrema*. (a) *M. nuwarense* (Hale 50 272). (b) *M. olivaceum* (Hale 50 145). (c) *M. polytretum* (Hale 50 238). (d) *M. porinaceum* (Hale 51 142). (e) *M. protoalbum* (Hale 51 044). (f) *M. rugiferum* (Hale 47 058). (g) *M. santessonii* (Wheeler 12 471 in US). (h) *M. subconforme* (Hale 50 510). (i) *M. terebrans* (Hale 47 202). See Fig. 7i for scale.

age; cortex dense, 15–18 μm, with conspicuous aculeate hyphae; algal layer continuous, 15 μm; medulla 180–200 μm with penetrations to 400 μm in eroding pockets of periderm; apothecia very numerous, immersed in the medulla, 0·2–0·3 mm diam, exciple fused, often free apically, colourless, pore round, 0·05–0·08 mm diam, becoming white rimmed and somewhat raised; hymenium 60–80 μm; spores colourless, transversely septate, 4–6 × 10–15 μm, 4 loculate, I+.

CHEMISTRY. 'Olivacea' unknowns (2 P− spots).

HABITAT. Canopy branches in rain forest at low to mid elevations (150–800 m).

DISTRIBUTION. West Indies, Central and South America, Sri Lanka, New Caledonia, Marquesas Islands.

ADDITIONAL SPECIMENS. Hale collections: 1 (50 226), 3a (46 291, 46 294, 46 352, 46 354), 4 (50 375), 6 (47 056, 47 190, 47 197, 47 203, 47 213), 7a (50 145), 7b (51 003, 51 029, 51 059, 51 073, 51 084, 51 253), 8 (47 007), 9 (46 138, 46 141, 46 145, 46 184, 46 185, 46 187, 47 007). Thwaites collections: Lgt. 75 as '*Thelotrema leptoporum*' (BM, S). Matara District: E of Gandara, *Santesson* 25 735 (S).

OBSERVATIONS. This canopy-dwelling species is essentially pantropical. The chemistry is distinctive although the identity of the two presumed depsidone components is still unknown. It is most often compared with *M. album* (e.g. Müller Argoviensis, 1887 : 7), which lacks any chemistry and has a much thinner thallus. The alleged olivaceous colour is probably taken from the type; fresh material is whitish or pale greenish mineral gray. Furthermore, as mentioned above, *M. microporum* cannot be considered a synonym of this species since it contains psoromic acid (P+ yellow). Another canopy species, *M. terebratulum*, should be recognized as distinct on the same basis. While *M. olivaceum* is widespread in the rain forest of Sri Lanka, it is curious that I found it only once in the extensive Weddagala logging area, showing how non-randomly the species may occur in a continuous forested area.

28. **Myriotrema polytretum** Hale **sp. nov.**

(Fig. 14c)

Thallus corticola, epiphloeodes, viridi-cinereus, 6–8 cm latus; apothecia numerosa, emersa, 0·3 mm diam, exciputo apice libero; ostiolum rotundatum, 0·1 mm diametro; hymenium 40–45 μm altum; sporae incolores, transversim septatae, octonae, 4 × 12 μm, 4 loculatae, I+ coeruleae.

Typus: Sri Lanka, Sabaragamuwa Province, Kegalla District, elev. 800 m Maliboda to Theberton, 16 Mar. 1978, *M. E. Hale* 50 238 (US—holotypus; BM—isotypus).

Thallus light greenish mineral gray, 6–8 cm broad, shiny, continuous; cortex very dense, 10 μm, with aculeate hyphae and some internal splitting; algal layer 15 μm; medulla 40–80 μm, with numerous crystals; apothecia common, immersed in the medulla, 0·2–0·3 mm diam, the exciple fused but partially free at the tips, pale orange red; pore round, *c.* 0·1 mm diam; hymenium 40–45 μm; spores colourless, transversely septate, 4 × 12 μm, 4 loculate, I+.

CHEMISTRY. 'Thwaitesii' unknown (P+ red).

HABITAT. Tree trunks along trail in mossy forest (900 m).

DISTRIBUTION. Sri Lanka, Malaya, Sarawak.

ADDITIONAL SPECIMENS. Hale collections: Malaya, Selangor, 30 271 (US); Sarawak, Sibu, 30 434 (US)

OBSERVATIONS. Externally *M. polytretum* is very similar to *M. album*, but I am separating it largely on the basis of the unusual chemistry (*M. album* lacks chemistry) and the thicker thallus.

29. **Myriotrema porinaceum** (Müll. Arg.) Hale in *Mycotaxon* **11** : 134 (1980).
(Fig. 14d)

Thelotrema porinaceum Müll. Arg. in *Nuovo G. bot. ital.* **23** : 130 (1891). Type: Japan, Awa, *Miyoshi* 17 (G—lectotype; FH—probable isolectotype).

Thallus greenish mineral gray, 3–6 cm broad, dull and thin, continuous; cortex loosely organized, 10 μm; algal layer discontinuous, 10 μm; medulla to 10 μm but mostly hypophloeodal; apothecia dispersed, semi-emergent but inconspicuous, 0·7–0·9 mm diam, the thalline rim lacking periderm cells, exciple fused, colourless; pore round, 0·05 mm diam, more or less white rimmed; hymenium 280–300 μm; spores colourless, muriform, 20–30 × 60–180 μm, with numerous locules, 1/ascus, I+.

Chemistry. Norstictic acid.

Habitat. Lower trunk of trees along trails at mid elevations or lower (350–850 m).

Distribution. Sri Lanka, Japan, Australia.

Additional specimens. Hale collections: 2 (51 142), 4 (50 305).

Observations. Norstictic acid as the main constituent is very rare in *Myriotrema*, known so far only in *M. norsticticum* (Hale) Hale and *M. occultum* (Eschw.) Hale from the New World; pantropical *M. compunctum* has stictic acid intermixed. *Myriotrema porinaceum* is a rather inconspicuous lichen since the sparsely developed, semi-emergent apothecia have a tiny pore and blend into the background of the thallus. Müller Argoviensis had compared the species with '*Thelotrema reclusum* Nyl.' (= *Myriotrema reclusum* (Krempelh.) Hale), a stictic acid-containing species from the Andaman Islands (see Hale, 1978*a* : 54).

30. **Myriotrema protoalbum** Hale **sp. nov.**
(Fig. 14e)

Thallus corticola, epiphloeodes, continuous, obscure viridis, 4–8 cm latus; apothecia immersa, inconspicua, 0·1–0·2 mm diametro, excipulo connato; hymenium 30–40 μm altum; sporae incolores, transversim septatae, 3–7 × 8–18 μm, 4 loculatae, I−.

Typus: Sri Lanka, Western Province, Kalatura District, Ambalam-pole, Morapitiya, elev. 300 m, 13 Mar. 1978, *M. E. Hale* 51 044 (US—holotypus; BM—isotypus).

Thallus dark greenish gray, 4–8 cm broad, shiny, continuous; cortex very dense, 11–14 μm, with short aculeate hyphae; algal layer continuous, 8–10 μm; medulla 10–30 μm, with crystals, mostly hypophloeodal; apothecia numerous but inconspicuous, 0·1–0·2 mm diam, immersed in part in the periderm, becoming slightly raised and darkening, the exciple fused, colourless; pore round, 0·01 mm diam, the rim whitish yellow; hymenium 30–40 μm; spores colourless, transversely septate, 3–7 × 8–18 μm, 4 loculate, I−.

Chemistry. No substances present.

Habitat. Lower trunk in rain forest at lower elevations (300–800 m).

Distribution. Sri Lanka.

Additional specimens. Hale collections: 1 (50 247), 2 (51 219).

Observations. The tiny apothecia are sometimes arranged in rows. The thallus is very thin and dark compared with *M. album* to which it seems to be related. It also falls close to *M. cinereoglaucescens*, a larger species.

31. **Myriotrema rugiferum** (Harm.) Hale in *Mycotaxon* **11** : 135 (1980).
(Fig. 14f)

Thelotrema rugiferum Harm. in *Bull. Séanc. Soc. Sci. Nancy* III, **13** : 44 (1912). Type: New Caledonia, *Pionniero* s.n. (DUKE—lectotype; S—isolectotype).

Thallus ashy greenish white, 7–15 cm broad, shiny, continuous; cortex dense, 15 μm, with well developed aculeate hyphae, splitting and exfoliating; algal layer continuous, 10–15 μm; medulla rather thick, 50–150 μm, with numerous crystals; apothecia numerous, immersed in the medulla, 0·3–0·4 mm diam, the exciple free apically, colourless, often visible through the pore; pore round, 0·1–0·15 mm diam, white rimmed; hymenium 60–90 μm; spores colourless, muriform, 4–6 × 9–20 μm, 1–3 × 3–5 loculate, I+.

CHEMISTRY. Psoromic acid with or without norpsoromic acid.

HABITAT. Mainly the lower trunks but also into the canopy in rain forest at all elevations (150–2100 m).

DISTRIBUTION. India, Sri Lanka, Philippines, New Caledonia, Solomon Islands.

ADDITIONAL SPECIMENS. Hale collections: 1 (50 232, 50 246), 2 (51 222), 3a (46 364), 4 (47 085, 47 150, 47 160, 50 373, 50 377, 50 428, 50 459, 50 504), 5 (46 232, 46 243, 46 256, 46 257, 46 262), 7b (50 310), 10 (50 279, 50 290). Thwaites collections: CL. 11 (BM, H-Nyl. 3889, S, UPS), C. L. 142 (BM, PDA) (as 'Lgt. 79. *T. concretum*'), C. L. 144 (BM, mixed with *Myriotrema thwaitesii*) as 'Lgt. 76. *T. microporum*').

OBSERVATIONS. In view of Salisbury's (1978 :412) recent treatment of *Thelotrema* (*Myriotrema*) *clandestinum*, I re-examined all of the material in US, some 52 collections. I confirmed that Fée's type in G has muriform spores (see Hale, 1978*a* : 41). I also found that there are two different populations. One of these, which I presume to be the typical population, occurs only in the New World and has a dull surface without exfoliating layers, few crystals in the medulla, and a generally 'hidden' exciple, that is the tips of the exciple do not protrude into the pore as an inner ring. The other population, which occurs throughout the Old World and in Panama, has an exfoliating cortex, numerous large crystals in the medulla, and a conspicuous exciple visible in the pore. This population is *M. rugiferum.*

Leighton used 'Lindig, Lich. Nov. Gran. 59' to identify C. L. 11 and C. L. 142 as *Thelotrema concretum* Fée (= *Myriotrema concretum* (Fée) Hale). The Lindig collection (BM and FH-Tuck.) contains psoromic acid and is correctly identified as *Myriotrema clandestinum* (Fée) Hale. While *M. concretum* also contains psoromic acid, there are fairly recognizable differences between the two species in apothecial characters, as outlined by Salisbury (1978 : 413).

32. **Myriotrema santessonii** (Hale) Hale in *Mycotaxon* **11** : 135 (1980). (Fig. 14g)

Thelotrema santessonii Hale in *Phytologia* **26** : 417 (1973). Type: Ivory Coast, Man, *Santesson* 10443 bis (UPS—holotype: US—isotype).
ICONES. Hale, 1973*b* : 420 fig. 8.

Thallus greenish ashy, *c.* 6 cm broad, shiny, with numerous hollow pustular outgrowths *c.* 1 mm high, 0·3–0·5 mm diam; cortex dense, 10–12 μm, with some aculeate hyphae, splitting and exfoliating; algal layer continuous, 15 μm; medulla to 60 μm with dense crystals; apothecia not seen (in type specimen immersed, 0·1–0·3 mm diam, the exciple fused, colourless; pore round *c.* 0·1 mm diam; hymenium 80–90 μm; spores colourless, muriform, 10–13 × 20–24 μm, 1–2 × 6–8 loculate, I— (apothecial characters taken from the type collection).

CHEMISTRY. Stictic and constictic acids.

HABITAT. On *Ficus* in disturbed areas at lower elevations (200 m).

DISTRIBUTION. Ivory Coast, Tanzania, Sri Lanka, Java.

ADDITIONAL SPECIMENS. Ratnapura District, Ratnapura, *Wheeler* 12471 (US).

OBSERVATIONS. Although the single Sri Lankan specimen lacks apothecia, the chemistry and characteristic pustules are sufficient for a tentative identification. The apothecial characters given here are based on the type (Hale, 1973*b* : 417).

33. **Myriotrema subconforme** (Nyl.) Hale in *Mycotaxon* **11** : 135 (1980).
(Fig. 14h)

Thelotrema subconforme Nyl. in *J. Linn. Soc. Bot.* **20** : 53 (1883). Type: Malaya, Malacca, May 1864, *Maingay* 64 (BM—lectotype; H-Nyl. 22587 (as no. 77), FH-Tuck., G—isolectotypes).

Thallus pale greenish gray, 6–8 cm broad, shiny, continuous, rather fragile; cortex dense, 10–15 μm, with aculeate hyphae, splitting into layers 5 μm thick; algal layer continuous, 15–18 μm; medulla 10–90 μm, with crystals; apothecia numerous, immersed to slightly raised, 0·2–0·3 mm diam, the exciple fused, colourless; pore round, 0·07–0·1 mm diam; hymenium 60–70 μm; spores colourless, muriform, 5–6 × 10–18 μm, 1–3 × 4–6 loculate, I+.

CHEMISTRY. No substances present.

HABITAT. Lower trunk to canopy of trees in rain forest at lower elevations (150–350 m).

DISTRIBUTION. India, Sri Lanka, Malaya, Philippines, Java, Sarawak, Solomon Islands.

ADDITIONAL SPECIMENS. Hale collections: 4 (50 510), 7a (50 192), 9 (46 162). Matara District, Dikwella, *Santesson* 25 744 (S).

OBSERVATIONS. This Asian species is closest to *M. album*. Nylander compared it to *Thelotrema conforme* Fée (= *Myriotrema conforme* (Fée) Hale), a New World species with psoromic acid.

34. **Myriotrema terebrans** (Nyl.) Hale in *Mycotaxon* **11** : 135 (1980).
(Fig. 14i)

Thelotrema terebrans Nyl. in *Bull. Soc. Linn. Normandie* II, **7** : 166 (1873). Type: India, Andaman Islands, 1867, *Kurz* 80 (H-Nyl. 22771—lectotype; BM, UPS, ZT—isolectotypes).
Ocellularia terebrans (Nyl.) Zahlbr., *Cat. Lich. Univers.* **2** : 602 (1923).

Thallus ashy mineral gray, 4–6 cm broad, shiny, continuous; cortex very dense, 10–12 μm, with conspicuous aculeate hyphae, splitting into sheets internally; algal layer continuous, 10 μm; medulla to 60 μm with inclusions of cortical layers and crystals; apothecia numerous, immersed in the medulla, the exciple poorly developed, fused, colourless; hymenium 45–65 μm; spores colourless, transversely septate, 4–5 × 10–15 μm, 4–6 loculate, I+.

CHEMISTRY. Stictic and constictic acids.

HABITAT. Canopy branches in rain forest at lower elevations (150–450 m).

DISTRIBUTION. India, Sri Lanka.

ADDITIONAL SPECIMENS. Hale collections: 6 (47 202), 8 (47 002).

OBSERVATIONS. *Myriotrema terebrans* has not been mentioned in the literature since Nylander's original publication. It is in the '*Thelotrema album*' group and can be distinguished by the chemistry. On the world level there are no comparable stictic acid-containing species.

35. **Myriotrema terebratulum** (Nyl.) Hale in *Mycotaxon* **11** : 135 (1980).
(Fig. 15a)

Thelotrema terebratulum Nyl. in *Annls Sci. nat.* (Bot.) V, **7** : 315 (1867). Type: Colombia, Rio Negro, 1863, *Lindig* 129 (H-Nyl. 22637—lectotype; FH-Tuck., G, PC—isolectotypes).
Ocellularia terebratula (Nyl.) Müll. Arg. in *Mém. Soc. Phys. Hist. nat. Genève* **29**(8) : 12 (1887).
Ocellularia galactina Zahlbr. in *Annls Cryptog. exot.* **5** : 216 (1932). Type: South Africa, Cape Province, Knysna, Jan. 1928, *van der Byl* 673 (W—lectotype; LD—isolectotype).
ICONES. Hale, 1974*a* : 26 fig. 13e (lectotype) and fig. 13i.—Hale, 1978*a* : 32 fig. 8d.

Thallus ashy greenish gray, 8–14 cm broad, smooth and shiny, continuous; cortex very dense, about 30 μm, with abundant aculeate hyphae, splitting and exfoliating, the layers about 4 μm thick; algal layer continuous, 15 μm; medulla 50–200 μm with remnants of cortical layers and crystals; apothecia numerous, immersed in the medulla, *c.* 0·2 mm diam, the exciple partially free at the tips, colourless, sometimes visible through the pore; pore round, about 0·05 mm diam, white rimmed; hymenium 60–70 μm; spores colourless, transversely septate, 4–7 × 9–15 μm, 3–4 loculate, I+.

CHEMISTRY. Psoromic and norpsoromic acids.

HABITAT. Tree trunks along open trails and in canopy in rain forest at low to mid elevations (300–850 m).

DISTRIBUTION. United States, West Indies, Central and South America, South Africa, India, Sri Lanka, Taiwan, Sabah, New Caledonia, Solomon Islands.

ADDITIONAL SPECIMENS. Hale collections: 1 (50 222), 3a (46 310), 4 (50 493). Thwaites collections: C. L. 145 (BM, PDA), C. L. 174 (PDA), C. L. 175 (BM, PDA) (as 'Lgt. 87, *Thelotrema myriotrema*') (mixtures of *Thelotrema platysporum* and *Myriotrema desquamans* in BM and UPS).

OBSERVATIONS. This is one of the most characteristic canopy-inhabiting lichens in the tropics. Its relationship to *M. album, M. microporum,* and *M. olivaceum* is discussed above under these names. Nylander mentioned two other confusable species in his original description: *Thelotrema microporellum* Nyl. (= *Myriotrema microporellum* (Nyl.) Hale), which contains hypoprotocetraric acid (Hale, 1978*a* : 24), and *Thelotrema plurifarium* Nyl., which I consider to be a synonym of *M. microporellum.*

Leighton called C. L. 174 *T. myriotrema* Nyl. (*Th. album* Fée), identifying it from his set of Wright's Lichenes Cubae no. 127 but not sending it on to Nylander for confirmation. The specimen is a mixture of *M. terebratulum* and *Thelotrema platysporum* (BM). The Cuban material (n. 127) contains hypoprotocetraric acid and can be determined as *M. microporellum.*

36. **Myriotrema thwaitesii** Hale **sp. nov.**

(Fig. 15b)

Thallus corticola, epiphloeodes, opacus, continuus, cinereo-albus, 8–10 cm latus; apothecia numerosa, dispersa, immersa, 0·2–0·3 mm diametro, excipulo incolore, columella nulla; ostiolum rotundatum, 0·05–0·08 mm diametro, albo-cinctum; hymenium 80–90 μm altum; sporae incolores, transversim septatae, octonae, 5–8 × 13–22 μm, 5–7 loculatae, I+ coeruleae.

Typus: Sri Lanka, Sabaragamuwa Province, Kegalla District, Maliboda to Theberton, elev. 800 m, 16 Mar. 1978, *M. E. Hale* 50 221 (US—holotypus; BM—isotypus).

Thallus pale greenish to yellowish gray, 8–12 cm broad, dull, continuous; cortex loosely organized and irregularly pored, 15–18 μm; algal layer continuous, 10–15 μm; medulla to 10 μm, mostly hypophloeodal; apothecia numerous, immersed in part in the periderm, 0·2–0·3 mm diam, the exciple fused, reddish brown, columella lacking; pore round, 0·05–0·08 mm diam, becoming white rimmed; hymenium 80–90 μm; spores colourless, transversely septate, 5–8 × 13–22 μm, 5–7 loculate, I+.

CHEMISTRY. 'Thwaitesii' unknown (P+ orange red).

HABITAT. Trees along trail and on lower trunks in rain forest at low to mid elevations. (150–1100 m).

DISTRIBUTION. Sri Lanka.

ADDITIONAL SPECIMENS. Hale collections: 1 (50 256), 5 (46 282), 9 (46 194). Thwaites collections: C. L. s.n. (PDA), C. L. 144 (BM, mixed with *Myriotrema clandestinum*) (as 'Lgt. 76. *T. microporum*').

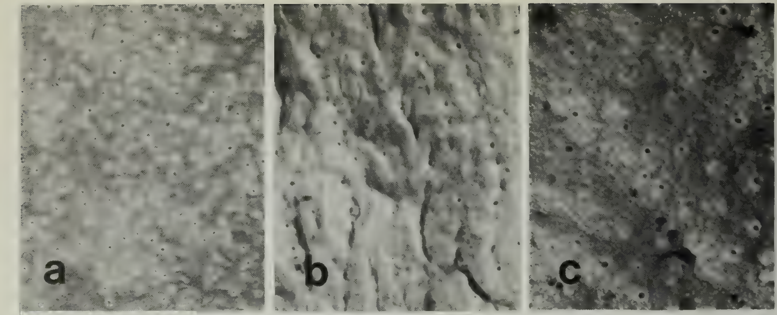

Fig. 15 Species of *Myriotrema*. (a) *M. terebratulum* (Hale 50 222). (b) *M. thwaitesii* (Hale 50 221). (c) *M. wightii* (Wheeler 12 465 in US). See Fig. 7i for scale.

OBSERVATIONS. The dull appearance of the thallus surface can be correlated with the poorly organized cortex. This trait, together with the P+ unknown, sets the species apart from others in the *M. album* complex. The substance reacts H_2SO_4+ dull orange and falls a little below the 'praestans' unknown from Dominica (see Hale, 1974*a* : 12). It may be related to thamnolic acid.

37. Myriotrema wightii (Taylor) Hale in *Mycotaxon* **11** : 135 (1980).
(Fig. 15c)

Endocarpon wightii Taylor in *Lond. J. Bot.* **6** : 155 (1847). Type: India, Madras, *Wight* s.n. (FH–Tayl.—lectotype; BM, G—isolectotypes).
Thelotrema subconcretum Leighton in *Trans. Linn. Soc. Lond.* **27** : 169 (1869). Type: Sri Lanka, Peradeniya, *Thwaites* C. L. 172 (BM—lectotype; G, NY, PC, PDA, S, UPS, W—isolectotypes).
Leptotrema wightii (Taylor) Müll. Arg. in *Flora, Jena* **65** : 499 (1882).
For additional synonymy see Sailsbury, 1971*a* : 5 and Hale, 1974*a* : 43 and 1978*a* : 55.
ICONES. Redinger, 1936 : 112 fig. 71—Salisbury, 1971*a* : 6 fig. 1.—Hale, 1978*a* : 55 fig. 15a (erroneously given as fig. 15b).

Thallus pale tannish mineral gray, 4–7 cm broad, thick and almost coriaceous, shiny, smooth and continuous, grainy; cortex lacking, a heavily pored polysaccharide sheet covering the underlying tissues; medulla dense and cellular, to 600 μm, organized in vertical blocks with algae in columns, with or without deep red crystalline masses, dense colourless crystals also present; apothecia immersed in the medulla, 0·2–0·3 mm diam, the exciple fused, often poorly developed; pore round, 0·05–0·1 mm diam, white rimmed; hymenium 180–200 μm; spores brown, muriform, 10–14 × 14–18 μm, 2 × 4 loculate, uniseriate, I–.

CHEMISTRY. No substances present except for K+ purple pigment.

HABITAT. On *Diospyros ebenum* in shade at low elevations.

DISTRIBUTION. United States, West Indies, Mexico, Central and South America, Portugal, India, Sri Lanka, Philippines, Sarawak, Australia, Hawaii.

ADDITIONAL SPECIMENS. N. Central Province, Wilpattu National Park, *Wheeler* 12 463 (US). Thwaites collections: C. L. 123 (H-Nyl. 3888, PDA).

OBSERVATIONS. Salisbury (1971*a* : 5) discussed this species fully. The red medullary crystals may rarely be absent. The thallus is coarse and thick. I did not collect it in the rain forests of Sri Lanka; it occurs in drier secondary forests.

III. **OCELLULARIA** G. Meyer, nom. cons.

Nebenstund : 327 (1825).

Ascidium Fée, *Essai Crypt.* : XLII (1824) (*nom. gen. rejic.*).
Porophora G. Meyer, *Nebenstund.* : 326 (1825).
Ectolechia Massal., *Alcun Gen. Lich.* : 10 (1855).
Leptotrema Mont. & Bosch in Junghuhn, *Pl. Junghuhn.* **4** : 483 (1855).
Stegobolus Mont., *Syll. Gen. Sp. Crypt.* : 362 (1856).
Macropyrenium Hampe in Massal. in *Atti R. Ist. veneto Sci.* III, **5** : 329 (1860).
Rhabdodiscus Vainio in *Suomal. Tiedeakat. Toim.* A, **15**(6) : 184 (1921).

Thallus crustose, epiphloeodal or rarely hypophloeodal; cortex dense, often splitting and exfoliating, or less commonly loosely organized, lacking in hypophloeodal species; medulla well developed to nearly hypophloeodal; apothecia emergent or rarely immersed, with a distinct thalline rim, the rim incurved to suberect, usually forming a discrete pore; exciple fused, carbonized; central columella often present, carbonized, simple to becoming reticulate; spores colourless or brown, transversely septate or muriform, I+ blue or rarely I−.

TYPE SPECIES. *Thelotrema obturatum* Ach.

NUMBER OF SPECIES. About 200.

OBSERVATIONS. This genus forms the most homogeneous group in the family. A few species in Sri Lanka lack a columella (see discussion under *O. rhicnopora*); the majority have one. It is possible to subdivide the columellate species into those with a simple columella (in part Salisbury's '*T. discolor*' group and the '*T. cavatum*' group, these being separated by columella height : width ratio) and those with a reticulate columella (the '*T. discoideum*' group) (Salisbury, 1978 : 407). There are, however, many transitional stages between these types, and I have not attempted to classify the species in this way.

Key to the species

1	Spores colourless		2
–	Spores brown		34
2	Spores transversely septate		3
–	Spores muriform		24
3	Spores large, 70–200 μm long		4
–	Spores small to medium sized, 20–65 μm		8
4	Central columella present		5
–	Central columella lacking		7
5	Thallus distinctly verruculose; no lichen substances present	8. **O. dolichotata**	
–	Thallus smooth to weakly verruculose; lichen substances present		6
6	'Olivacea' unknown present	26. **O. nylanderiana**	
–	Hypoprotocetraric acid present	41. **O. triglyphica**	
7	Hypoprotocetraric acid present	25. **O. neopertusariiformis**	
–	'Pertusariiformis' unknown present	30. **O. pertusariiformis**	
8	Medulla wholly or in part orange	33. **O. punctulata**	
–	Medulla white		9
9	Pore rim and tip of columella pale orange		10
–	Pore rim and tip of columella white, blackening, or concolourous with the thallus		11
10	Medulla P+ yellow (psoromic acid present)	15. **O. lankaensis**	
–	Medulla P– ('chonestoma' unknown present)	6. **O. croceopora**	
11	Thallus dull, lacking a cortex; pore area usually darkening	34. **O. pyrenuloides**	
–	Thallus shiny, corticate; pore area concolourous or white		12
12	Central columella present		13
–	Central columella lacking		23
13	No lichen substances present on t.l.c.; medulla P–		14
–	Lichen substances always present; medulla P+ orange or red (P— only in *O. chonestoma*)		16
14	Apothecia flush to barely raised, 0·4–0·7 mm diam	28. **O. papillata**	
–	Apothecia emergent, 0·8–1·2 mm diam		15
15	Spores 40–65 μm long	27. **O. orthomastia**	

– Spores 18–30 μm long . . . . 2. **O. ascidioidea**
16 Medulla P—('chonestoma' unknown present) . . . . . . 4. **O. chonestoma**
– Medulla P+ orange or red 17
17 Pore gaping, to 0·7 mm wide; thalline rim suberect; columella broad, becoming reticulate . . . . 9. **O. emersa**
– Pore smaller, 0·05–0·2 mm diam; thalline rim incurved; columella narrow, simple . 18
18 Apothecia large and emergent, 1–1·3 mm diam . . . . . . 15. **O. lankaensis**
– Apothecia smaller, less than 1 mm wide, not strongly emergent 19
19 Pore coarsely white rimmed; 'cinchonarum' unknown present . . 24. **O. neocavata**
– Pore not strongly white rimmed; 'cinchonarum' unknown lacking 20
20 Medulla P+ yellow (psoromic acid present) . . . . 31. **O. pluripora**
– Medulla P+ orange or red (psoromic acid lacking) 21
21 Stitic acid present on t.l.c. . . . . 37. **O. sticticans**
– Stictic acid lacking 22
22 Protocetraric acid present on t.l.c. . . . . 29 **O. perforata**
– 'Diacida' unknown present on t.l.c. . . . . 7. **O. diacida**
23 Pore area concolourous with the thallus; hypoprotocetraric acid present on t.l.c. 13. **O. kanneliyensis**
– Pore area brownish, wrinkled; no substances present . . . . . 36. **O. rhicnopora**
24 Spores large, 100–360 μm long 25
– Spores small, less than 30 μm long 28
25 Central columella present . . . . 19. **O. massalongoi**
– Central columella lacking 26
26 Apothecia somewhat raised to emergent, 0·6–1·0 mm diam; pore small, 0·1 mm diam . . . . 14. **O. keralensis**
– Apothecia emergent to strongly emergent, 1–1·3 mm diam; pore larger, to 0·2 mm diam 27
27 Spores turning brownish at maturity; no lichen substances present 23. **O. monosporoides**
– Spores colourless at maturity; hypoprotocetraric acid present . . 10. **O. eumorpha**
28 Central columella lacking; disc orange yellow pruinose . . . . 3. **O. aurata**
– Central columella present; disc not visible or white pruinose 29
29 Thallus dull, whitish gray, cortex lacking 30
– Thallus shiny, whitish green; cortex present 32
30 Columella much wider than high; pore 0·2–0·3 mm diam . . 16. **O. leucomelaena**
– Columella narrow, higher than wide; pore less than 0·1 mm diam 31
31 Thallus P+ orange (stictic acid present) . . . . 22. **O. melanotremata**
– Thallus P– (no substances present) . . . . 39. **O. tenuis**
32 Columella reticulate at maturity; pore gaping, 0·2–0·4 mm diam . 32. **O. polillensis**
– Columella simple; pore smaller, 0·1–0·2 mm diam 33
33 Protocetraric acid present on t.l.c. . . . . 38. **O.subsimilis**
– Fumarprotocetraric acid present on t.l.c. (with traces of protocetraric acid) 40. **O. thelotremoides**
34 Apothecia elongate at maturity . . . . 17. **O. lirelliformis**
– Apothecia round 35
35 Thallus dull, whitish gray; cortex lacking. 36
– Thallus shiny, whitish green; cortex present 37
36 Columella narrow, 60–180 μm diam; apothecia raised . . . 21. **O. meiospermoides**
– Columella broader, to 300 μm diam, becoming reticulate; apothecia flush . . . . 20. **O. meiosperma**
37 Apothecia deeply immersed in periderm; pore very tiny, to 0·5 mm diam. 11. **O. exuta**
– Apothecia not deeply immersed, raised at maturity; pore 0·1 mm diam, white rimmed . . . . 35. **O. rassagala**
38 Spores large, 120–210 μm long . . . . 23. **O. monosporoides**
– Spores small, 10–30 μm long 39
39 Columella simple 40
– Columella becoming reticulate at maturity 41
40 Thallus verruculose and white spotted; spores 22–30 μm . . 1. **O. albomaculata**
– Thallus smooth, not spotted; spores 12–20 μm . . . . . 18. **O. marivelensis**
41 Thalline rim suberect, often jagged . . . . 5. **O. crassa**
– Thalline rim more or less incurved, entire . . . . 12. **O. fissa**

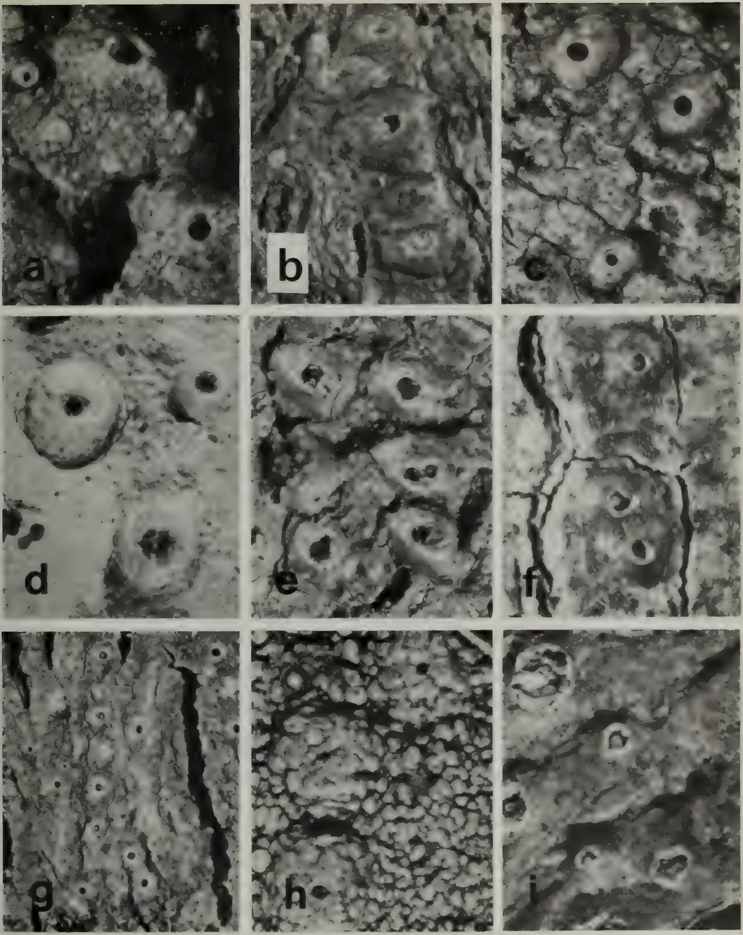

Fig. 16 Species of *Ocellularia*. (a) *O. albomaculata* (Hale 46 140). (b) *O. ascidioidea* (Hale 47 035). (c) *O. aurata* (Hale 51 521). (d) *O. chonestoma* (Hale 46 394). (e) *O. crassa* (Hale 47 076). (f) *O. croceopora* (Hale 46 129). (g) *O. diacida* (Hale 50 258). (h) *O. dolichotata* (Hale 46 210). (i) *O. emersa* (Hale 50 145). See Fig. 7i for scale.

1. **Ocellularia albomaculata** Hale **sp. nov.**
(Fig. 16a)

Thallus corticola, epiphloeodes, verruculosus, continuus vel fissurinus, nitidus, viridi-albus, ad 10 cm latus; apothecia emergentia, 0·8–1·2 mm diametro, amphithecio verrucoso, excipulo fuligineo, columella 250–300 μm diametro; ostiolum rotundatum, 0·2–0·4 mm diametro, albo-cinctum; hymenium 150–180 μm altum; sporae fuscae, murales, 9–10 × 22–30 μm, 1–2 × 4 loculatae, uniseriatae, I+ coeruleae.

Typus: Sri Lanka, Southern Province, Kanneliya Forest Reserve southeast of Hiniduma, 16 Feb. 1976, *M. E. Hale* 46 140 (US—holotype; AMH, PDA—isolectotypes).

Thallus pale greenish gray, up to 10 cm broad, finely verrucose, shiny, continuous to fissured; cortex dense, 12–15 μm, splitting with some exfoliation; algal layer 15–18 μm, more or less continuous between crystals; medulla 80–150 μm, with large crystal masses to 100 μm wide; apothecia emergent, 0·8–1·2 mm diam, the amphithecium verruculose, exciple carbonized; columella present, 250–300 μm broad; hymenium 150–180 μm; spores brown, muriform, 9–10 × 22–30 μm, 1–2 × 4 loculate, uniseriate, I+.

CHEMISTRY. No substances present.

HABITAT. Mid bole to canopy of trees in rain forest at low elevations (150 m).

DISTRIBUTION. Sri Lanka.

ADDITIONAL SPECIMENS. Hale collections: 9 (46 148).

OBSERVATIONS. This species is characterized by the greenish, shiny, verruculose, grainy and spotted cortex and the gaping pore through which the top of the columella is visible.

2. **Ocellularia ascidioidea** Hale **sp. nov.**
(Fig. 16b)

Thallus corticola, epiphloeodes, continuus, aetate rimosus, cinereo-albus, 6–10 cm latus; apothecia numerosa, solitaria, emergentia, 0·8–1·0 mm diametro, epithecio fuligineo, columella 150–190 μm diametro, fusca; ostiolum rotundatum, 0·2–0·3 mm diametro; hymenium 150–190 μm altum; sporae octonae, incolores, transversim septatae, 5–8 × 18–30 μm, 6–8 loculatae, I+ coeruleae.

Typus: Sri Lanka, Southern Province, Matara District, Morawaka Hill southwest of Deniyaya, 15 Feb. 1976, *M. E. Hale* 47 035 (US—holotypus; BM—isotypus).

Thallus whitish mineral gray, 6–10 cm diam, shiny, continuous; cortex dense, 8–10 μm; algal layer 10–15 μm; medulla variable, 10–20 μm, mostly hypophloeodal; apothecia numerous, moderately emergent, 0·8–1·0 mm diam, the exciple carbonized; columella distinct, 150–190 μm diam; pore 0·2–0·3 mm diam, often filled with tip of columella; hymenium 150–190 μm; spores colourless, transversely septate, 5–8 × 18–30 μm, 6–8 loculate, I+.

CHEMISTRY. No substances present.

HABITAT. Lower bole, rarely into the canopy, in rain forest at 150–600 m elevation.

DISTRIBUTION. Sri Lanka.

ADDITIONAL SPECIMENS. Hale collections: 4 (47 082), 7b (51 066), 8 (47 012), 9 (46 175).

OBSERVATIONS. This species has clearly emergent apothecia and a well developed columella. The most closely related species, *O. papillata*, has flush to barely raised apothecia and a variable, often weakly developed columella.

3. **Ocellularia aurata** (Tuck.) Hale in *Mycotaxon* **11** : 136 (1980).
(Fig. 16c)

Thelotrema auratum Tuck. in *Proc. Am. Acad. Arts Sci.* **5** : 408 (1862). Type: Cuba, *Wright* 133 (FH-Tuck.—lectotype; BM, G, L, PC, UPS—isolectotypes).

For additional synonymy see Hale (1978*a* : 40).
ICONES. Hale 1978*a* : 5 fig. 1f (lectotype).

Thallus greenish to whitish gray, 5–10 cm broad, shiny, fissured; cortex dense, variably thickened, 18–30 μm; algal layer continuous, 15 μm; medulla to 90 μm with crystals; apothecia conspicuous, strongly emergent, 0·8–1·2 mm diam, the exciple carbonized; columella lacking; pore gaping, 0·2–0·4 mm diam, disc and inner walls pale yellowish to orange-red pruinose; hymenium 100–110 μm; spores colourless, muriform, 6–8 × 12–18μm, 1–2 × 4–5 loculate, I+.

CHEMISTRY. Protocetraric acid and unidentified K+ purple pigments.

HABITAT. Canopy branches in rain forest at lower elevations (150–350 m).

DISTRIBUTION. West Indies, Central and South America, Sri Lanka, Philippines, Sarawak, New Caledonia, Samoa, Solomon Islands.

ADDITIONAL SPECIMENS. Hale collections: 3a (46 308), 4 (47 124, 50 521), 9 (46 212).

OBSERVATIONS. This pantropical species generally occurs in the canopy in rain forest at low elevations. The pigmented disc is easily seen through the large pore.

4. Ocellularia chonestoma (Leighton) Zahlbr., *Cat. Lich. Univers.* **2** : 586 (1923). (Fig. 16d)

Thelotrema chonestomum Leighton in *Trans. Linn. Soc. Lond.* **27** : 171 (1870). Type: Sri Lanka, south of island, *Thwaites* 168 (BM—lectotype; G, PC, PDA, UPS, W, isolectotypes)..

Thallus ashy whitish to tannish mineral gray, 8–15 cm broad, shiny, continuous; cortex weakly developed and irregularly pored, up to 8 μm thick with some aculeate hyphae; algal layer 10 μm; medulla mostly hypophloeodal, embedded between periderm layers; apothecia numerous and conspicuous, strongly emergent and in part basally constricted, 0·8–1·5 mm diam, the amphithecium with a thick medulla easily abraded and exposed, exciple carbonized; columella well developed, 90–300 μm diam; pore round, 0·2–0·5 mm diam; hymenium 90–140 μm; spores colourless, transversely septate, 5–6 × 18–30 μm, 6–8 loculate, I+.

CHEMISTRY. 'Chonestoma' unknown and the upper 'olivacea' unknown (P—).

HABITAT. Base, lower bole, saplings, rarely into the canopy in rain forest at lower elevations (150–800 m).

DISTRIBUTION. Sri Lanka, Philippines, Sarawak, Sabah, Solomon Islands.

ADDITIONAL SPECIMENS. Hale collections: 1 (50 231, 50 233, 50, 235, 50 257), 3a (46 309, 46 313, 46 324, 46 344, 46 378), 4 (47 109, 50 399, 50 415, 50 417, 50 421, 50 494, 50 522), 6 (47 079, 47 089, 47 108, 47 149, 47 157, 47 164, 47 167, 47 174, 47 185, 47 216), 7a (50 179, 50 184), 7b (50 299, 50 311, 51 001), 9 (46 133, 46 157, 46 176, 46 193, 46 197, 46 204, 46 206, 46 219, 46 394). Thwaites collections: C. L. 269 (PDA), C. L. s.n. (BM PDA (as 'Lgt. 101, *Ascidium chonestomum*'), C. L. 169 (BM, PDA, UPS) (as 'Lgt. 88, *T. cavatum* var. *confertum*').

OBSERVATIONS. This is the most common member of the family in Sri Lanka. Although it occurs, much less commonly, in dipterocarp forest as far east as the Solomon Islands, there are no records from neighbouring India. One character not mentioned by Leighton is the tendency for the emergent apothecia to become abraded, revealing the thick, pure white medulla of the amphithecium and contrasting strongly with the tannish green thallus.

The 'chonestoma' unknown is a H_2SO_4+ gray spot above the 'olivacea' series in hexane system. These two P— compounds are probably closely related depsides or depsidones.

Leighton's determination of '*T. cavatum* Nyl., var. *confertum* Nyl.' proved to be *O. chonestoma*. The name, not checked by Nylander, appears to have been taken from a comparison of the Sri Lankan material with Lindig's Colombia collection so named by Nylander. This taxon, *Ocellularia conferta* (Nyl.) Dodge, is a psoromic acid-containing member of *Myriotrema* and may be a good species.

5. **Ocellularia crassa** (Müll Arg.) Hale in *Mycotaxon* **11** : 136 (1980).
(Fig. 16e)

Leptotrema crassum Müll. Arg. in *Flora, Jena* **65** : 332 (1882). Type: Java, *Junghuhn* 158 (L—lectotype; H-Nyl., G—isolectotypes).

Leptotrema fallax Müll Arg. in *Flora, Jena* **70** : 62 (1887). Type: Australia, Richmond River, *Hodgkinson* s.n. (G—lectotype).

Leptotrema integrum Müll. Arg. in *Flora, Jena* **70** : 399 (1887). Type: Australia, Queensland, *Sayer* s.n. (G—lectotype).

Thelotrema vesiculiferum Vainio in *Suomal. Tiedeakat. Toim.* A, **15**(6) : 175 (1921). Type: Philippines, Prov. Sorsogon, Irosin, Dec. 1915, *Elmer* 1406 (TUR—lectotype; FH, US, W—isolectotypes).

Leptotrema vesiculiferum (Vainio) Zahlbr., *Cat. Lich. Univers.* **2** : 641 (1923).

Thallus greenish mineral gray, 4–12 cm broad, shiny, continuous; cortex dense, 12–15 μm, with some aculeate hyphae; algal layer continuous, 15–20 μm; medulla 10–100 μm, with dense crystals; apothecia semi-emergent, the thalline wall becoming suberect, the rim jagged, exciple carbonized; columella entire to reticulate, 140–250 μm diam, the tip white pruinose; pore gaping, 0·2–0·4 mm diam; hymenium 65–90 μm; spores brown, muriform, 5–10 × 9–15 μm, 1–2 × 3–5 loculate, I–.

CHEMISTRY. Psoromic acid with or without norpsoromic acid.

HABITAT. Base to mid trunk of trees in rain forest at low to mid elevations (150–850 m).

DISTRIBUTION. Sri Lanka, Philippines, Java, Sabah, Australia.

ADDITIONAL SPECIMENS. Hale collections: 1 (50 208, 50 236), 2 (51 103, 51 117, 51 125, 51 131, 51 155, 51 160, 51 190, 51 210), 3a (46 295), 3b (46 386), 4 (47 074, 47 076, 47 104, 47 215, 50 429), 5 (46 275).

OBSERVATIONS. As in other genera in the family, the species with psoromic acid tend to form intergrading aggregates. The large synonymy I propose reflects the problems in defining columellar development, degree of emergence of the thalline wall, and variation in pore width. I have here defined *O. crassa* as having a greenish, shiny thallus, relatively thick cortex (although the thallus appears thin under a hand lens), jagged, suberect thalline rim, and gaping pore. It occurs at lower elevations.

Ocellularia crassa has frequently been compared (and confused) with *O. fissa* (see below). Müller Argoviensis considered *O. crassa* to be near *O. fissa,* although I doubt that he saw the Nylander type. Externally *O. fissa* appears to have a thicker thallus, even though it is not much, if at all, thicker when measured against *O. crassa*. It also has a more whitish colour and less emergent apothecia with a smooth rim. Finally it seems to occur at higher elevations, above the range of *O. crassa.*

6. **Ocellularia croceopora** Hale **sp. nov.**
(Fig. 16f)

Thallus corticola, epiphloeodes, continuus vel fissus, nitidus, pallide viridi-albus, 8–15 cm latus; apothecia numerosa, prominentia, emergentia, solitaria vel rare 2 : nae aggregata, 0·9–1·2 mm diametro, columella 180–230 μm; ostiolum rotundatum, 0·2–0·4 mm diametro, profundum, vix albo-annulatum, margine et apice columellae pallide croceo; hymenium 65–120 μm altum; sporae incolores, tranversim septatae, octonae, 3–5 × 9–15 μm, 4 loculatae, I+ coeruleae.

Typus: Sri Lanka, Southern Province, Galle District, Kanneliya Forest Reserve, elev. 150 m, 16 Feb. 1976, *M. E. Hale* 46 129 (US—holotypus; BM—isotypus).

Thallus greenish to whitish mineral gray, 8–15 cm broad, shiny; cortex dense, 12–18 μm, with aculeate hyphae, splitting into layers internally; algal layer continuous, 15–20 μm; medulla to 10 μm, mostly hypophloeodal; apothecia common, emergent, 0·9–1·2 mm diam, the exciple carbonized, columella 180–230 μm; pore round, 0·2–0·4 mm diam, columella surface and inner wall pale orange; hymenium 65–120 μm; spores colourless, transversely septate, 3–5 × 9–15 μm, 4–5 loculate, I+.

Chemistry. 'Chonestoma' unknowns (P−).

Habitat. Base and lower trunk, rarely into the canopy, in rain forest at lower elevations (150–200 m).

Distribution. Sri Lanka.

Additional specimens. Hale collections: 9 (46 151, 46 169, 46 181, 46 186, 46 201, 46 209, 46 214).

Observations. *Ocellularia croceopora* is very similar to *O. lankaensis* externally, with a pale orange-pruinose pore area but smaller spores and different chemistry (*O. lankaensis* has psoromic acid). Curiously the species was collected frequently at Hiniduma in the Kanneliya Forest Reserve but at no other localities. At the same time *O. lankaensis* was represented at most of the low elevation localities but only once at Hiniduma.

7. **Ocellularia diacida** Hale in *Mycotaxon* 7 : 378 (1978).
(Fig. 16g)

Type: India, Karnataka, Devimane Ghat, evergreen forest, 26 Feb. 1977, *M. E. Hale* 47933 (US—holotype; AMH—isotype).

Icones. Hale, 1978*b* : 384 fig. 2.

Thallus greenish to dull brownish gray, to 10 cm broad, dull, smooth to fissured with age; cortex dense, 8–10 μm; algal layer continuous, 15–18 μm; medulla up to 20 μm thick, mostly hypophloeodal; apothecia numerous, nearly flush to semi-emergent, 0·3–0·4 mm diam, the exciple fused, reddish brown; columella 45–50 μm diam; pore round, 0·1 mm diam, white rimmed; hymenium 110–130 μm; spores colourless, transversely septate, 5–6 × 15–30 μm, 7–8 loculate, I+.

Chemistry. Unknown substances ('diacida' unknowns, P−).

Habitat. Tree trunks along trail at mid elevations (800 m).

Distribution. India, Sri Lanka.

Additional specimens. Hale collections: 1 (50 258).

Observations. The single specimen from Sri Lanka is identical with the Indian population. I can add nothing new about the identity of the unknown spot, a H_2SO_4+ brown double spot near norstictic. The species is probably related to *O. perforata*, which contains protocetraric acid.

8. **Ocellularia dolichotata** (Nyl.) Zahlbr., *Cat. Lich. Univers.* **2** : 589 (1923).
(Fig. 16h)

Thelotrema dolichotatum Nyl., *Sert. Lich. Trop. Labuan Singapore* : 19 (1891). Type: Singapore, Nov. 1879, *Almquist* s.n. (H-Nyl. 22748—lectotype; S—isolectotype).
Thelotrema siamense Vainio in *Hedwigia* **47** : 175 (1907). Type: Thailand, Ko Chang, Klong Sarlakpet, 1900, *Schmidt* XXXVII (TUR—lectotype; C—isolectotype).
Ocellularia siamensis (Vanio) Zahlbr., *Cat. Lich. Univers.* **2** : 600 (1923).

Thallus ashy white, 8–12 cm broad, shiny, verruculose and grainy; cortex cellular, 10–20 μm thick, with some aculeate hyphae; algal layer 10 μm; medulla variable, to 10 μm, with numerous crystals, largely hypophloeodal; apothecia rather sparse, emergent, densely verruculose, 1·1–1·4 mm diam, the exciple carbonized; columella 150–300 μm diam; pore round, 0·1–0·2 mm diam; hymenium 200–250 μm; spores colourless, transversely septate, 15–20 × 120–200 μm, 12–15 loculate, 2/ascus, I+.

Chemistry. No substances present.

Habitat. Base to mid bole, rarely into the canopy, in rain forest at low elevations (100–300 m).

Distribution. Sri Lanka, Thailand, Peninsular Malaysia, Philippines, Sabah, Sarawak, Solomon Islands.

Additional specimens. Hale collections: 3a (46 296), 4 (47 098), 9 (46 146, 46 161, 46 183, 46 196, 46 210).

Observations. This Asian species is characterized by the large apothecia and strongly verruculose thallus, or as Nylander described it, 'minute granulato-rugatulus'. Vainio differentiated his *Thelotrema siamense* from *T. dolichotatum* by the presence of a columella and asci with 2–3 spores. In fact Nylander's type also has a columella, and while the spores in *T. siamense* are reported to be 12–14 × 30–110 μm, a measurement which I confirmed, they appear to be immature; the hymenium is infested with a parasitic fungus.

9. **Ocellularia emersa** (Krempelh.) Müll. Arg. in *Flora, Jena* **69** : 310 (1886). (Fig. 16i)

Thelotrema emersum Krempelh. in *Flora, Jena* **59** : 221 (1876). Type: Brazil, *Glaziou* 3189 (M—lectotype; C, G, H, UPS, W—isolectotypes).

Thelotrema efformatum Krempelh. in *Flora, Jena* **59** : 221 (1876). Type: Brazil, *Glaziou* 3190 (M—lectotype; C, G, H, UPS, W—isolectotypes).

Thelotrema schizostomum Krempelh. in *Flora, Jena* **59** : 222 (1876) (non Tuck. ex anno 1862). Type: Brazil, *Glaziou* 3260 (M—lectotype; C, H, UPS, W—isolectotypes).

Ocellularia efformata (Krempelh.) Müll. Arg. in *J. Linn. Soc.* (Bot.) **30** : 452 (1895).

Ocellularia emersella Müll. Arg. in *J. Linn. Soc.* (Bot.) **30** : 453 (1895) (Based on *Thelotrema schizostomum*).

Phaeotrema emersum (Krempelh.) Zahlbr. in *Denkschr. Akad. Wiss. Wien* (Math.-nat. Kl.) **83** : 119 (1909).

Icones. Redinger, 1936 : 40, 41 figs 17, 18.

Thallus pale whitish green to yellowish gray, 6–10 cm broad, shiny, continuous; cortex dense, 8–10 μm, with aculeate hyphae, splitting and exfoliating; algal layer continuous, 15 μm; medulla 15–30 μm, with large crystals; apothecia common, semi-emergent with a suberect, rarely somewhat recurved thalline rim, round to irregular, 0·5–1·0 mm diam, the exciple carbonized; columella variable, in part reticulated, 60–200 μm diam, apically pruinose; pore variable, 0·1–0·7 mm diam; hymenium 60–75 μm; spores colourless, transversely septate, 4–5 × 9–12 μm, 5–7 loculate, I+.

Chemistry. Psoromic and norpsoromic acids.

Habitat. Lower trunks of trees in rain forest at lower elevations (150–300 m).

Distribution. West Indies, Central and South America, Sri Lanka.

Additional specimens. Hale collections: 4 (47 143), 7a (50 148), 7b (51 022, 51 047, 51 068), 9 (46 191, 46 200). Thwaites collections: C. L. 166 (BM, PDA), C. L. 269 (PDA) (as 'Lgt. 78, *Thelotrema platystomum*', mixed with *Ocellularia fissa*).

Observations. Redinger (1936 : 39) has discussed this species rather thoroughly, considering *Thelotrema efformatum* to be a synonym since the alleged spore difference—smaller spores in *T. efformatum*, according to Krempelhuber—did not hold up on re-examination. *Ocellularia emersa* is indeed variable in terms of development of the thalline rim and degree of reticulation of the columella, and we may be dealing with more than one species on the world level. Zahlbruckner (1909 : 119) was correct in seeing a relation between this species and *Phaeotrema virens* Müll. Arg. (= *Ocellularia virens* (Müll. Arg.) Hale).

The Thwaites material was mixed, part being *Ocellularia emersa*, part *O. fissa*. Leighton had identified it as '*T. platystomum* Mont.' without the benefit of Nylander's advice. An isotype of *O. platystomum* (Mont.) Zahlbr. in H-Nyl. (*Leprieur 491*, French Guyana), however, lacks any chemistry, has a non-reticulated columella, and is apparently hypophloeodal. It cannot be characterized beyond this until better collections are seen.

10. **Ocellularia eumorpha** (Stirton) Hale in *Mycotaxon* **11** : 136 (1980).
(Fig. 17a)

Thelotrema eumorphum Stirton in *Proc. phil. Soc. Glasg.* **10** : 158 (1877). Type: India, Kumaon, *Dictrie* s.n. (BM—lectotype).

Thallus pale yellowish or straw coloured, 5–12 cm broad, shiny, smooth to rugulose; cortex loosely cellular, 15–20 μm; algal layer continuous, 10–15 μm; medulla 0–30 μm with small crystals, mostly hypophloeodal; apothecia emergent to strongly emergent, solitary to loosely clumped in twos or threes, 1–1·3 mm diam, the exciple carbonized; columella lacking; pore round, 0·1–0·13 mm diam, white rimmed and sometimes depressed; hymenium 280–300 μm; spores colourless, muriform, 25–35 × 150–180 μm, with numerous locules, 1–2/ascus, I+.

Chemistry. Hypoprotocetraric and 4-O-demethylnotatic acids (see Culberson & Hale, 1973).

Habitat. Lower trunks in rain forest at low to mid elevations or higher (150–2100 m).

Distribution. India, Sri Lanka.

Additional specimens. Hale collections: 2 (51 224), 5 (46 253), 9 (46 217), 10 (50 282).

Observations. *Ocellularia eumorpha* has large emergent apothecia and externally resembles *O. domingensis* (see below under *O. rhicnopora*). A related Asian species, *O. arecae* (Vainio) Hale, differs only in having a columella, a character that has not proved to be especially strong in other species. Stirton compared his species with *Thelotrema occlusum* Nyl., a New World species which coincidentally has hypoprotocetraric acid but differs strongly in having immersed apothecia and periphysoids. Salisbury (1971*b* : 277) listed *Thelotrema (Ocellularia) arecae* as a synonym of *T. interpositum* Nyl. (= *Ocellularia interposita* (Nyl.) Hale). However, *O. interposita* is a New World species with psoromic acid and a strongly verruculose thallus (Hale, 1974*a* : 35). Another synonym he gives, *T. sanfordianum* Zahlbr. (= *Ocellularia sanfordiana* (Zahlbr.) Hale), lacks any lichen substances and has a blackened pore area; it occurs only in the southern United States. A third synonym, *T. turgidulum* Vainio (Salisbury, 1971*b* : 278), may well be correct but I have not yet seen the type specimen.

11. **Ocellularia exuta** Hale **sp. nov.**
(Fig. 17b)

Thallus corticola, epiphloeodes, fragilis, continuus, 6–10 cm latus; apothecia profunde immersa, 0·2–0·3 mm diametro, excipulo fuligineo, columella 60 μm diametro; ostiolum rotundatum, 0·01–0·05 mm diametro; hymenium 150–160 μm altum; sporae fuscae, transversim septatae, octonae, 6–8 × 12–24 μm, 4–6 loculatae, I−.

Typus: Sri Lanka, Southern Province, Galle District, Kanneliya Forest Reserve, elev. 150 m, 16 Feb. 1976, *M. E. Hale* 46 158 (US—holotypus; BM, PDA—isotypi).

Thallus whitish mineral gray, 6–10 cm broad, growing on rotted bark and easily disintegrating, shiny, continuous; cortex dense but very thin, 5 μm, algal layer continuous, 15 μm; medulla 10–20 μm with crystals, mostly hypophloeodal; apothecia inconspicuous, deeply immersed in the periderm, 0·2–0·3 mm diam, the exciple carbonized; columella *c*. 60 μm

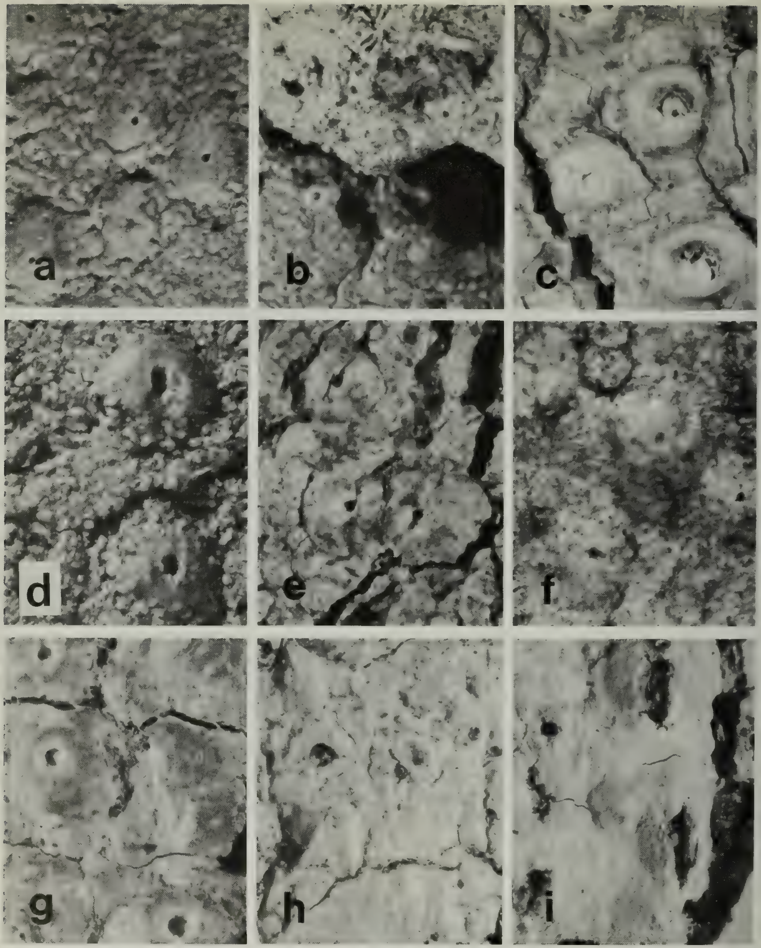

Fig. 17. Species of *Ocellularia*. (a) *O. eumorpha* (Hale 51 224). (b) *O. exuta* (Hale 46 158). (c) *O. fissa* (Hale 50 283). (d) *O. kanneliyensis* (Hale 46 213). (e) *O. keralensis* (Nagarkar & Gole 76 542 in US). (f) *O. keralensis* (Hale 46 281). (g) *O. lankaensis* (Hale 47 184). (h) *O. leucomelaena* (Hale 50 294). (i) *O. lirelliformis* (Hale 51 092). See Fig. 7i for scale.

diam; pore round, 0·01–0·05 mm diam, narrowly white rimmed; hymenium 150–160 μm; spores brown, transversely septate, 6–8 × 18–24 μm, 4–6 loculate, uniseriate, I–.

Chemistry. Psoromic acid.

Habitat. Canopy branches in rain forest at lower elevations (300 m).

Distribution. Sri Lanka.

Additional specimens. Hale collections: 9 (46 136).

Observations. This unique species has immersed apothecia with a tiny pore and a fragile thallus growing on crumbling bark. It occupies the same habitat as *Thelotrema platysporum* in the rain forest. There are no related species.

12. **Ocellularia fissa** (Nyl.) Hale in *Mycotaxon* **11** : 136 (1980).
(Fig. 17c)

Thelotrema fissum Nyl. in *Annls Sci. nat.* (Bot.) IV, **11** : 258 (1859). Type: Bourbon [= Réunion], *Richard* s.n. (H-Nyl. 229659—lectotype; G, PC—isolectotypes).
Trypethelium schizostomum Leighton in *Trans. Linn. Soc. Lond.* **27** : 184 (1870). Type: Sri Lanka, Central Province, *Thwaites* C. L. 121 (BM—lectotype; H-Nyl. 7562, G, PDA, S—isolectotypes) (duplicates as Lgt. 192 in BM, S = *Myriotrema fluorescens*).
Leptotrema fissum (Nyl.) Müll. Arg. in *Flora, Jena* **65** : 333 (1882).
Leptotrema sandwicense Zahlbr. in *Annls mycol.* **10** : 372 (1912). Type: Hawaii, Oahu, Mt. Punaluu, *Rock* 60 (W—lectotype).
Rhabdodiscus fissus (Nyl.) Vainio in *Suomal. Tiedeakat. Toim. A*, **15**(6) : 184 (1921).
Thelotrema schizostomoides Zahlbr., *Cat. Lich. Univers.* **2** : 628 (1923). Based on *Trypethelium schizostomum* [Non *Thelotrema schizostomum* Tuck. ex anno 1862, nec Krempelh. ex anno 1876.]
Leptotrema oleosum Zahlbr. in *Bot. Mag., Tokyo* **61** : 317 (1927). Type: Japan, Yakushima, July 1906, *Faurie* 2415 (W—lectotype; KYO—isolectotype).
Icones. Hale, 1974*a* : 41 fig. 19a (lectotype) and fig. 19c.

Thallus whitish or tannish gray, 6–10 cm broad, shiny, continuous to fissured with age; cortex dense but rather thin, 8–10 μm, with aculeate hyphae; algal layer continuous, 15 μm; medulla 20–60 μm, with crystals; apothecia semi-emergent, 0·7–1·1 mm diam, the thalline rim becoming suberect, entire, exciple carbonized; columella more or less reticulate, 60–100 μm diam, the pruinose tip often filling the pore; pore gaping at maturity, 0·2–0·6 mm diam; hymenium 90–120 μm; spores brown, muriform, 6–7 × 8–15 μm, 1–2 × 3–4 loculate, I–.

Chemistry. Psoromic acid with or without norpsoromic acid.

Habitat. Tree trunks in open forest at higher elevations (2100–2200 m).

Distribution. West Indies, Mascarene Islands, Sri Lanka, Japan, Solomon Islands, Hawaii.

Additional specimens. Hale collections: 10 (50 275, 50 283), 11 (50 325, 50 327), 12 (50 362). Thwaites collections: C. L. 166 (BM, PDA, S, UPS) (as 'Lgt. 78. *Thelotrema platystomum*') (mixture with *Ocellularia emersa*). Almquist collections: Pidurutalagala, *Almquist* s.n. (H-Nyl., S) (as '*Thelotrema epitrypum*').

Observations. Nylander presented the basic features of this species in his original description: 'margo thallinus firmus erectus vel nonnihil connivens'. Zahlbruckner emphasized the thick thallus, although as I pointed out above it is not really much thicker than that of *O. crassa*, a confusable relative at lower elevations in Sri Lanka. As with *O. crassa*, this psoromic acid-containing species is extremely variable and I cannot claim that the treatment presented here is final.

Nylander identified the Almquist collection as '*Thelotrema epitrypum* Nyl. N. Gran. p. 49'. That species, which incidentally also contains psoromic acid (*Lindig 2769*, isolectotype in FH-Tuck.), has small, emergent apothecia (0·4–0·6 mm diam) with a simple, narrow columella. It is not at all related to *O. fissa*.

13. **Ocellularia kanneliyensis** Hale **sp. nov.**
(Fig. 17d)

Thallus corticola, epiphloeodes, verruculosus granulosusque, tenuis, pallide olivaceus, 8–12 cm latus; apothecia dispersa, separata, valde emergentia, basin constricta, 1·2–1·5 mm diametro, excipulo apice fuligineo, columella nulla; ostiolum rotundatum, 0·3–0·5 mm diametro, nigro-cinctum; hymenium 140–150 μm altum; sporae incolores, transversim septatae, octonae, 6–7 × 24–33 μm, 6–8 loculatae, I+ coeruleae.

Typus: Sri Lanka, Southern Province, Galle district, Kanneliya Forest Reserve, elev. 150 m, 16 Feb. 1976, *M. E. Hale* 46 213 (US—holotypus).

Thallus pale brownish to olive gray, 8–12 cm broad, densely verruculose to granular, continuous; cortex very dense, 15–20 μm; algal layer 10 μm; medulla about 10 μm, bulging out with crystals inclusions in the verrucae, mostly hypophloeodal; apothecia sparse, strongly emergent, 1·2–1·5 mm diam, the exciple carbonized; columella lacking; pore round to irregular, 0·3–0·5 mm diam; hymenium 140–150 μm; spores colourless, transversely septate, 6–7 × 24–33 μm. I+.

CHEMISTRY. Hypoprotocetraric acid and a lower unidentified spot (?4-O-demethylnotatic acid).

HABITAT. Mid bole of trees in rain forest at low elevations (150 m).

DISTRIBUTION. Sri Lanka.

ADDITIONAL SPECIMENS. Hale collections: 9 (46 166).

OBSERVATIONS. *Ocellularia kanneliyensis* can be recognized by the granular thallus and large, emergent apothecia which lack a columella. Another species in Sri Lanka with hypoprotocetraric acid, *O. neopertusariiformis*, has larger apothecia and large spores (80–155 μm long). On the world level, *O. domingensis* (Nyl.) Müll Arg., known from the New World (Hale, 1978*a* : 20), differs in having a smooth thallus, almost urceolate apothecia, and very large spores (150–210 μm long). This same evolutionary series includes *O. eumorpha* (see above).

14. **Ocellularia keralensis** Patwardhan & C. Kulkarni ex Hale **sp. nov.**
(Figs 17e, f)

Thallus corticola, epiphloeodes, stramineo-albidus, nitidus, verruculosus, aetate rimosus, 8–16 cm latus; apothecia dispersa, semi-emergentia, 0·6–1·0 mm diametro, excipulo fuligineo, columella nulla; ostiolum rotundatum, *c.* 0·1 mm diametro, depressum, anguste nigro-cinctum; hymenium 200–300 μm altum; sporae incolores, murales, 25–45 × 100–210 μm, dense loculatae, 1 : nae, I+ coeruleae.

Typus: India, Kerala, Munnar-Kodai road below Gellapatti, 1 Jan. 1976, *M. B. Nagarkar & K. D. Gole* 76·542 (AMH—holotypus; US—isotypus).

Thallus pale tannish gray, 8–16 cm broad, shiny, verruculose, fissured with age; cortex irregularly developed and pored, 10–15 μm; algal layer continuous, 15 μm; medulla to 50 μm but mostly hypophloeodal; apothecia dispersed, becoming emergent or remaining barely semi-emergent, 0·6–1·0 mm diam, the exciple carbonized apically; columella lacking; pore round, *c.* 0·1 mm diam, becoming narrowly black rimmed and depressed; hymenium 200–300 μm; spores colourless, muriform, 25–45 × 100–210 μm, with numerous locules, 1/ascus, I+.

CHEMISTRY. No substances present.

HABITAT. Lower trunks into the canopy of trees in rain forest at low to mid elevations (150–1100 m)

Distribution. India and Sri Lanka.

Additional specimens. Hale collections: 1 (50 215), 3a (46 292, 46 319, 46 326, 46 355), 4 (47 075, 47 080, 47 087, 47 114), 5 (46 224, 46 231a, 46 225, 46 260, 46 264, 46 269, 46 274, 46 281), 8 (47 041).

Observations. While first recognized from India, where it occurs in the Western Ghats, *O. keralensis* is more common in the rain forests of Sri Lanka. It is an inconspicuous species with small-pored, sometimes barely raised apothecia. I know of no similar species in the genus.

15. **Ocellularia lankaensis** Hale **sp. nov.**
(Fig. 17g)

Thallus corticola, epiphloeodes, viridi-glaucescens, 8–16 cm latus; apothecia emergentia, 1–1·3 mm diametro, excipulo fuligineo, columella centrali 90–320 μm diametro; ostiolum rotundatum, 0·2–0·3 mm diametro, pallide croceum; hymenium 90–120 μm altum; sporae incolores, transversim septatae, octonae, 4–7 × 10–22 μm, 5–7 loculatae, I+ coerulaea.

Typus: Sri Lanka, Western Province, Kalutara District, near Hedigalla, Morapitiya, elev. 150 m, 11 Feb. 1976, *M. E. Hale* 47 184 (US—holotypus; BM—isotypus).

Thallus pale greenish mineral gray, 8–16 cm broad, shiny, smooth to verruculose, fissured with age; cortex dense, 10–15 μm, with aculeate hyphae, splitting into several layers internally; algal layer continuous, 10–15 μm; medulla 30–60 μm with abundant deposits of psoromic acid and oxalate crystals; apothecia numerous, emergent, 1–1·3 mm diam, the exciple carbonized; columella 90–320 μm diam, the tip and pore area usually distinctly orange pruinose, rarely white; pore round, 0·2–0·3 mm diam; hymenium 90–120 μm; spores colourless, transversely septate, 4–7 × 10–22 μm, 5–7 loculate, I+.

Chemistry. Psoromic acid with or without norpsoromic acid.

Habitat. Base, lower trunk, and saplings in rain forest at low to mid elevations (150–850 m).

Distribution. Sri Lanka.

Additional specimens. Hale collections: 2 (51 106, 51 110, 51 145, 51 153, 51 154, 51 180, 51 184, 51 234), 3a (46 320, 46 334, 46 340, 46 357, 46 366), 3b (46 385, 46 389), 4 (47 094, 47 095, 47 151, 50 407, 50 412, 50 490, 50 506), 6 (47 181), 7a (50 163, 50 165, 50 180), 7b (51 008, 51 065, 51 249), 8 (47 032), 9 (46 188). Thwaites collections: C. L. 124 (BM, H-Nyl. s.n., S, UPS) (as 'Lgt. 81, *T. olivaceum*') C. L. 262, 264, 265 (PDA).

Observations. This species has a conspicuous pale orange-pruinose pore area, although the colouration is lacking in a few specimens. A P+ yellow colour test will separate it from *O. croceopora* ('chonestoma' unknown present), a much rarer species with similar orange pruina. It has larger apothecia than other columellate psoromic acid-containing species such as *O. antillensis* Hale, *O. comparabilis* (Krempelh.) Müll. Arg., or *O. discoidea* (Ach.) Müll. Arg., none of which occur in Sri Lanka. I have not yet seen any material of *O. lankaensis* outside of Sri Lanka, where it is one of the most common species in the family.

Both Nylander and Leighton erred in identifying Thwaites C. L. 124 as '*T. olivaceum* Mont.' An isotype of Montagne's species in Genève is identical with *Myriotrema immersum* (Eschw.) Hale, which contains protocetraric acid.

16. **Ocellularia leucomelaena** (Nyl.) Hale in *Mycotaxon* **11** : 137 (1980).
(Fig. 17h)

Thelotrema leucomelaenum Nyl. in *Acta Soc. Scient. fenn.* 7 : 452 (1863). Type: Colombia, *Lindig* 2777 (H-Nyl. 22576—lectotype; BM, FH-Tuck., G—isolectotypes).

Icones. Redinger, 1936 : 92 fig. 55.—Hale, 1974*a* : 37 fig. 17a (lectotype) and fig. 17d.—Hale, 1978*a* : 40 fig. 121.

For additional synonymy see Hale, 1974*a* : 36.

Thallus whitish mineral gray, *c.* 6 cm broad, dull, continuous; cortex weakly developed or lacking; algal layer 10–15 μm, discontinuous among superficial medullary hyphae; medulla mostly hypophloeodal; apothecia immersed, 0·6–0·8 mm diam, exciple carbonized; columella very wide, to 360 μm; pore round to irregular, 0·2–0·3 mm, black rimmed, black tip of columella clearly visible; hymenium 12 μm; spores colourless, muriform, 9 × 21–24 μm, 1–3 × 5–7 loculate, I−.

CHEMISTRY. No substances present.

HABITAT. Branches of trees at higher elevations (2100 m).

DISTRIBUTION. West Indies, Central and South America, Ivory Coast, Sri Lanka, Hawaii.

ADDITIONAL SPECIMENS. Hale collections: 10 (50 294).

OBSERVATIONS. Nylander reported the characteristic I− spore reaction in his original description and Redinger (1936 : 91) emphasized the broad columella. Although widespread in the New World, where I believed it to be endemic, we now have collections not only from Sri Lanka but also from the Ivory Coast (*Santesson* 10 658e in S).

17. **Ocellularia lirelliformis** (Tuck.) Hale in *Mycotaxon* **11** : 137 (1980).
(Fig. 17i)

Thelotrema lirelliforme Tuck. in *Proc. Am. Acad. Art Sci.* **6** : 270 (1864). Type: Cuba, *Wright* 150 (FH-Tuck.—lectotype; BM, H-Nyl. 22689, G, L, M, PC, UPS, US—isolectotypes).
Rhabdodiscus lirelliformis (Tuck.) Vainio in *Suomal. Tiedeakat. Toim.* A **15**(6) : 184 (1921).
Phaeotrema lirelliforme (Tuck.) Zahlbr., *Cat. Lich. Univers.* **2** : 608 (1923).

Thallus whitish mineral gray, 4–8 cm broad, dull, continuous to somewhat fissured; cortex not fully developed, 10–20 μm; algal layer 10–15 μm, interrupted by crystals; medulla mostly hypophloeodal; apothecia immersed, round to elongate, 0·8–1·3 mm long, the thalline rim suberect, rarely erect and slightly recurved, exciple carbonized; columella broad, to 0·6 mm broad, inner wall and disc black or becoming white pruinose; hymenium 120–150 μm; spores brown, transversely septate, 6–9 × 18–21 μm, 4 loculate, I−.

CHEMISTRY. No substances present.

HABITAT. Canopy of trees in rain forest at lower elevations (300 m).

DISTRIBUTION. West Indies, Central America, Sri Lanka.

ADDITIONAL SPECIMENS. Hale collections: 7b (51 035, 51 092).

OBSERVATIONS. Tuckerman compared this species with *Thelotrema auberianum* Mont. (= *Ocellularia auberiana* (Mont.) Hale) (see Hale, 1978*a* : 35), which has psoromic acid and a reticulate columella.

18. **Ocellularia marivelensis** (Vainio) Hale in *Mycotaxon* **11** : 137 (1980).
(Fig. 18a)

Thelotrema marivelense Vainio in *Suomal. Tiedeakat. Toim* A, **15**(6) : 176 (1921). Type: Philippines, Prov. Bataan, Mt Mariveles, Feb. 1905, *Whitford* 1088 (TUR-Vain. 26 772—lectotype; F, FH, US—isolectotypes).
Leptotrema marivelense (Vainio) Zahlbr., *Cat. Lich. Univers.* **2** : 637 (1923).

Thallus ashy green, 6–12 cm broad, appearing thick, shiny, continuous; cortex dense but thin, 5–10 μm, with aculeate hyphae, some splitting and exfoliation; algal layer 10–15 μm; medulla 30–50 μm with numerous crystals; apothecia semi-emergent, 0·8–1·2 mm diam, the exciple carbonized; columella variable, 120–310 μm diam, the white pruinose tip visible in the pore; pore rather open, 0·2–0·4 mm diam; hymenium 110–130 μm; spores brown, muriform, 8–12 × 12–20 μm, 1–2 × 4–7 loculate.

CHEMISTRY. Psoromic acid.

HABITAT. Canopy of trees in rain forest at low elevations (150–350 m).

DISTRIBUTION. India, Sri Lanka, Philippines, Fiji, Solomon Islands.

ADDITIONAL SPECIMENS. Hale collections: 4 (47 084, 47 123, 47 154, 50 148), 9 (46 130, 46 164).

OBSERVATIONS. This Asian species is obviously related to *O. crassa* and *O. fissa* (see above) but the columella lacks reticulations.

19. Ocellularia massalongoi ['massalongi'] (Mont.) Hale in *Mycotaxon* **11** : 137 (1980). (Fig. 18b).

Ascidium massalongoi ['Massalongi'] Mont. in *Annls Sci. nat.* (Bot.) IV, **14** : 174 (1860). Type: 'Ind. Or.' *s.c.* no. 94 (PC—lectotype).

Macropyrenium pertusarioides Hampe in Massal., *Esame Comp.*: 330 (1860). Type: Ceylon, *s.c.*, s.n. (H-Nyl. 22441a—lectotype?).

Ascidium monobactrium Nyl. in *Annls Sci. nat.* (Bot.) IV, **15** : 53 (1861). Type: Sabah, Labuan, Tonjong Kubong, *Motley* s.n. (H-Nyl. 22428b—lectotype; BM, PC—isolectotypes).

Ascidium pachystomum Leighton in *Trans. Linn. Soc. Lond.* **27** : 171 (1870). Type: Sri Lanka, South of Island, *Thwaites* C. L. 171 (BM—lectotype; G, NY, PC, PDA, S, UPS—isolectotypes).

Thelotrema pachystomum (Leighton) Müll. Arg. in *Flora, Jena* **74** : 112 (1891).

Thelotrema monobactrium var. *subgranulatum* Nyl., *Sert. Lich. Trop. Labuan Sing.* 6 : (1891). Type: Sabah, Labuan, Tonjong Kubong, *Motley* s.n. (H-Nyl. 22428—lectotype; BM (as no. 2)—isolectotype).

Thelotrema monobactrium (Nyl.) Vainio in *Suomal. Tiedeakat. Toim.* A, **15**(6) : 177 (1921).

Thelotrema marginans Vainio in *Suomal. Tiedeakat. Toim.* A, **15**(6) : 179 (1921). Type: Philippines, Biliran, June 1914, *R. MacGregor* Bur Sci. 18422 (TUR–Vain. 26 853—lectotype).

Thelotrema monobactrium var. *endoleucum* Vainio in *Suomal. Tiedeakat. Toim.* A, **15**(6) : 178 (1921). Type: Philippines, Prov. Sorsogon, Irosin, Nov. 1915, *Elmer* 15 050 (TUR—lectotype; BM, FH, G, L, LD, US, W—isolectotypes).

Thelotrema monobactrium var. *endorhoda* Vainio in *Suomal. Tiedeakat. Toim.* A, **15**(6) : 178 (1921). Type: Philippines, Prov. Sorsogon, Irosin, Nov. 1915, *Elmer* 15 078 (TUR—Vain. 26 826—lectotype; FH, L, US—isolectotypes).

Thelotrema monobactrium var. *geminipara* Vainio in *Suomal. Tiedeakat. Toim.* A, **15**(6) : 178 (1921). Type: Philippines, Prov. Sorsogon, Irosin, April 1916, *Elmer* 14 813 (FH, US—isotypes).

Thelotrema leightonii Zahlbr., *Cat. Lich. Univers.* **2** : 620 (1923). Based on *T. pachystomum* (Leighton) Müll. Arg., non *T. pachystomum* Nyl.

Thelotrema massalongoi ['*Massalongii*'] (Mont.) Zahlbr., *Cat. Lich. Univers.* **2** : 624 (1923).

Thallus dull greenish mineral gray, 8–14 cm broad, shiny, smooth and continuous; cortex dense, very thick, 30–40 μm, with aculeate hyphae, splitting internally into layers; algal layer continuous, 15–17 μm; medulla to 100 μm with crystals; apothecia strongly emergent, solitary or less commonly aggregated in twos, 1–1·3 mm diam, exciple carbonized; columella *c.* 300 μm diam; pore round, 0·08–0·1 mm diam, depressed but surrounded by a strongly raised rim; hymenium 300–400 μm; spores colourless, muriform 25–30 × 150–360 μm, with numerous locules, 1/ascus, I+.

CHEMISTRY. Salazinic acid.

HABITAT. Saplings and lower trunk to mid bole of trees in rain forest at lower elevations (150–350 m).

DISTRIBUTION. Sri Lanka, Malaya, Sabah, Philippines, Japan, Solomon Islands.

ADDITIONAL SPECIMENS. Hale collections: 3a (46 285, 46 361), 4 (50 376, 50 484), 7a (50 144, 50 160, 50 167, 50 173). Thwaites collections: C. L. 170 (BM, PDA) (as 'Lgt. 99. *A. pachystomum*').

OBSERVATIONS. *Ocellularia massalongoi* is easily recognized by the large apothecia with a

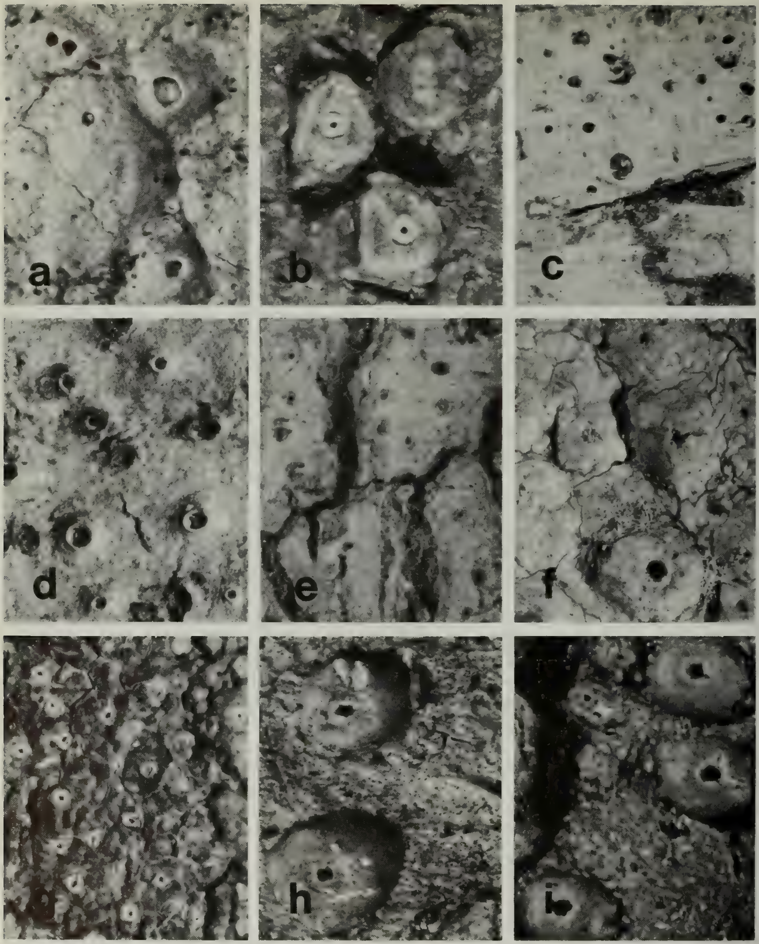

Fig. 18 Species of *Ocellularia*. (a) *O. marivelensis* (Hale 46 130). (b) *O. massalongoi* (Hale 50 484). (c) *O. meiosperma* (Almquist s.n. in S; isolectotype of *Thelotrema subinalbescens*). (d) *O. meiospermoides* (Hale 46 268). (e) *O. melanotremata* (Hale 46 241). (f) *O. monosporoides* (Hale 50 276). (g) *O. neocavata* (Hale 50 255). (h) *O. neopertusariiformis* (Hale 47 145). (i) *O. nylanderiana* (Hale 47 132). See Fig. 7i for scale.

raised rim around the pore, a trait mentioned by all earlier workers, and the chemistry. Salazinic acid is extremely rare in the family, known as far as I am aware in just *Ocellularia interponenda* (Nyl.) Hale, *O. massalongoi* and *Thelotrema hians* Stirton.

20. **Ocellularia meiosperma** (Nyl.) Hale in *Mycotaxon* **11** : 137 (1980).
(Fig. 17c)

Thelotrema meiospermum Nyl. in *Annls Sci. nat.* (Bot.) IV, **19** : 333 (1863). Type: Cuba, *Wright* 136 (FH-Tuck.—lectotype; BM, G, H-Nyl. 22858, L, PC, UPS—isolectotypes).
Phaeotrema meiospermum (Nyl.) Müll. Arg. in *Flora, Jena* **69** : 311 (1886).
Thelotrema subinalbescens Nyl. in *Acta Soc. Scient. fenn.* **26** : 18 (1900). Type: Sri Lanka, Pointe de Galle, *Almquist* s.n. (S—lectotype).
Verrucaria discissa Nyl. in *Acta Soc. Scient. fenn.* **26** : 25 (1900). Type: Sri Lanka, Pointe de Galle, *Almquist* s.n. (H-Nyl. 1361—lectotype).
Pyrenula discissa (Nyl.) Zahlbr., *Cat. Lich. Univers.* **1** : 428 (1921).
Phaeotrema subinalbescens (Nyl.) Zahlbr., *Cat. Lich. Univers.* **2** : 610 (1923).
For additional synonymy see Hale, 1978*a* : 36.
ICONES. Hale, 1978*a* : 35 fig. 9e.

Thallus whitish mineral gray, 1–2 cm broad, dull, continuous; cortex not clearly developed, a thin polysaccharide layer covering the surface; algal layer scattered among medullary hyphae; medulla 25–30 μm, with crystals; apothecia immersed, round to irregular, 0·2–0·4 mm diam, the exciple carbonized; columella broad, to 0·3 mm diam, becoming somewhat reticulated at maturity; hymenium 90–100 μm; spores brown, transversely septate, 10 × 16–20 μm, 4–5 loculate, I−.

CHEMISTRY. No substances present.

HABITAT. Secondary forest at low elevations (100 m).

DISTRIBUTION. United States, West Indies, Central America, Sri Lanka, Philippines, Java, Sarawak.

OBSERVATIONS. I did not collect this rather inconspicuous lichen in Sri Lanka. It is apparently confined to secondary lowland forests. Nylander described *Thelotrema subinalbescens* at the end of his career, saying 'affine *Th. phaeospermum* Nyl. in Wright. Cub. n : o 45', apparently an otherwise unpublished name. I have had no success in tracing the identity of the Cuban specimen. Dr P. G. Patwardhan (Poona) was the first to recognize *Verrucaria discissa* as a *Phaeotrema,* and he called my attention to it.

21. **Ocellularia meiospermoides** Hale **sp. nov.**
(Fig. 18d)

Thallus corticola, hypophloeodes, opacus, 8–10 cm latus; apothecia emergentia, solitaria, 0·6–1·0 mm diametro, exciputo fuligineo, columella 60–180 μm diametro; ostiolum rotundatum, 0·1–0·3 mm diametro, albo-cinctum; hymenium 110–130 μm altum; sporae fuscae, transversim septatae, octonae, 6–7 × 24–33 μm, 6–7 loculatae, I−.

Typus: Sri Lanka, Southern Province, Galle District, Kanneliya Forest Reserve, elev. 150 m, 16 Feb. 1976, *M. E. Hale* 46 268 (US—holotypus; BM, PDA—isotypi).

Thallus tannish mineral gray, 8–10 cm broad, dull, thin, continuous; cortex lacking; algae scattered among superficial medullary hyphae; medulla mostly hypophloeodal; apothecia emergent, solitary, 0·6–1·0 mm diam, the exciple carbonized; columella 60–180 μm; pore round, 0·1–0·3 mm diam, white rimmed; hymenium 110–130 μm; spores brown, transversely septate, 6–7 × 24–33 μm, 6–7 loculate, I−.

CHEMISTRY. No substances present.

HABITAT. Lower trunks of trees in rain forest at lower elevations (150–850 m).

DISTRIBUTION. Sri Lanka.

ADDITIONAL SPECIMENS. Hale collections: 2 (50 161).

OBSERVATIONS. I am describing this species on the basis of the distinctly emergent apothecia and the columella higher than wide. In other respects it is close to *O. meiosperma* (above).

22. **Ocellularia melanotremata** Hale **sp. nov.**
(Fig. 18e)

Thallus corticola, hypophloeodes, opacus, albo-cinereus, 4–12 cm latus; apothecia immersa vel vix semi-emergentia, 0·2–0·3 mm diametro, excipulo fuligineo, columella 45–60 μm; ostiolum rotundatum, 0·05–0·10 diametro, nigro-cinctum; hymenium 80–120 μm altum; sporae incolores, transversim septatae, 6–10 × 15–24 μm, 1–2 × 5–7 loculatae, 4–8 : nae, I–.

Typus: Sri Lanka, Southern Province, Matara District, mossy forest above Enselwatta, elev. 1100 m, 14 Feb. 1976, *M. E. Hale* 46 241 (US—holotypus; BM—isotypus).

Thallus whitish gray, 4–12 cm broad, very thin, dull, continuous; cortex lacking; algae scattered among superficial medullary hyphae; medulla mostly hypophloeodal; apothecia more or less immersed to barely emergent, 0·2–0·3 mm diam, the exciple carbonized; columella 45–60 μm diam; pore round, 0·05–0·1 mm diam, becoming black rimmed; hymenium 8–120 μm; spores colourless, transversely septate, 6–10 × 15–24 μm, 1–3 × 5–7 loculate, 4–8/ascus, I–.

CHEMISTRY. Stictic acid.

HABITAT. Saplings, base or lower trunks of trees in low to mid elevation rain forest (150–1100 m).

DISTRIBUTION. Sri Lanka.

ADDITIONAL SPECIMENS. Hale collections: 1 (50 241, 50 242), 2 (51 152), 4 (47 131, 50 413, 50 425, 50 472), 7a (50 169, 50 172, 50 174), 7b (51 012).

OBSERVATIONS. This ecorticate species is very close to *O. erumpens* (Magnusson) Hale (see Hale, 1978*a* : 43), which has larger spores (36–50 μm long) and apothecia (0·5–0·7 mm diam). It is rather common in the rain forests of Sri Lanka and will undoubtedly be found in the Indo-Malaysian area by future collectors.

23. **Ocellularia monosporoides** (Nyl.) Hale in *Mycotaxon* **11** : 137 (1980).
(Fig. 18f)

Thelotrema monosporoides Nyl., *Lich. New Zealand*: 76 (1888). Type: New Zealand, *Knight* s.n. (H-Nyl.—lectotype; G—isolectotype).
Leptotrema monosporoides (Nyl.) Müll Arg. in *Bull. Herb. Boissier* **2** (append. 1) : 75 (1894).

Thallus pale straw coloured, 2–6 cm broad, appearing thick, dull, smooth to verruculose, fissured; cortex dense, 15–20 μm; algal layer continuous, 10–15 μm; medulla 10–15 μm, with crystals, mostly hypophloeodal; apothecia semi-emergent, 1–1·3 mm diam, the exciple carbonized apically; columella lacking; pore variable, round, 0·1–0·3 mm diam, more or less depressed; hymenium 280–300 μm; spores nearly colourless to pale brown or darkening at maturity, muriform, 30–35 × 120–210 μm, with numerous locules, 1/ascus, I–.

CHEMISTRY. No substances present.

HABITAT. Trees in open forest at higher elevations (2100–2200 m).

DISTRIBUTION. Sri Lanka, New Zealand.

ADDITIONAL SPECIMENS. Hale collections: 10 (50 262, 50 265, 50 266, 50 276, 50 278, 50 285, 50 289, 50 291), 12 (50 346, 50 360). Thwaites collections: C. L. 141 (BM, PDA, S, UPS) (as 'Lgt. 95. *Ascidium depressum*'). Other collections: Horton Plains, *Moberg* 2619 (UPS), *Santesson* 25 862, 25 941, 26 028, 26 031 (S).

OBSERVATIONS. Nylander separated this species from *Thelotrema monosporum* by the larger spores (140–200 μm long) in his original description. A more basic difference, of course, is that *O. monosporoides* has a carbonized exciple and lacks periphysoids. The spores may be colourless well into the mature stages, and only slowly and imperfectly turn brown in Sri Lanka. Leighton misidentified the species as '*Ascidium depressum*' and failed to send a duplicate to Nylander for verification; *Thelotrema depressum* Mont. (see Hale, 1974*a* : 33) is a heavily carbonized, columellate species from the New World.

24. **Ocellularia neocavata** Hale **sp. nov.**
(Fig. 18g)

Thallus corticola, epiphloeodes, rugulosus, viridi-cinerascens, 8–12 cm latus; apothecia immersa, vel vix semi-emergentia, 0·3–0·4 mm diametro, excipulo pallide fuligineo, columella 60 μm diametro; ostiolum rotundatum, 0·1 mm diametro; hymenium 90 μm altum; sporae incolores, transversim septatae, octonae, 5 × 15–25 μm, 7–8 loculatae, I+ coeruleae.

Typus: Sri Lanka, Sabaragamuwa Province, Kegalla District, Maliboda to Theberton, elev. 800 m, 16 Mar. 1978, *M. E. Hale* 50 255 (US—holotypus; BM—isotypus).

Thallus pale greenish mineral gray, 8–12 cm broad, shiny, verruculose and rugulose, fissured; cortex dense, 15 μm; algal layer 15 μm; medulla to 150 μm under verrucae, with large crystals; apothecia numerous, immersed, flush to somewhat raised, 0·3–0·4 mm diam, the thalline rim jagged and white pruinose apically, exciple mostly fused, the tips filling the pore; columella 60 μm diam, weakly carbonized; pore round to irregular, partially closed, 0·1 mm diam; hymenium 90 μm; spores colourless, transversely septate, 5 × 15–25 μm, 7–8 loculate, I+.

HABITAT. Saplings along trail in rain forest at lower to mid elevations (300–800 m).

DISTRIBUTION. Sri Lanka.

ADDITIONAL SPECIMENS. Hale collections: 7b (51 240).

OBSERVATIONS. This species differs from *O. cavata* (Ach.) Müll. Arg. in having a semi-erect, white pruinose thalline rim with the apothecia barely raised. The walls and the columella are weakly carbonized. By comparison, *O. cavata* has emergent apothecia with a small, discrete pore and heavily carbonized exciple and columella. The chemistries are identical, a series of H_2SO_4+ gray spots between fumarprotocetraric and protocetraric acids. In Sri Lanka *O. punctulata* also has this chemistry and at the world level *O. cavata, O. crocea* (Krempelh.) v. Overeem & D. v. Overeem, *O. decolorata* Hale, *O. dodecamera* (Nyl.) Vainio, *O. exigua* Müll. Arg., *O. polydisca* Redinger, *O. rhabdospora* (Nyl.) Redinger, *O. subemersa* Müll Arg., *O. xanthostromiza* (Nyl.) Zahlbr., and one species with muriform spores, *O. neodominicana* Hale (see Hale, 1974*a* : 33, under *Thelotrema dominicanum*). No species of *Myriotrema* or *Thelotrema* are known to contain this substance.

25. **Ocellularia neopertusariiformis** Hale **sp. nov.**
(Fig. 18h)

Thallus corticola, epiphloeodes, albo-viridis vel cinereus, 8–12 cm latus; apothecia valde emergentia, basin constricta, 1·5–1·9 mm diametro, excipulo fuligineo, columella nulla; ostiolum rotundatum, 0·2–0·4 mm diametro, nigro-cinctum; hymenium 210 μm altum; sporae incolores, transversim septatae, 12–22 × 80–155 μm, 24–37 loculatae, 2–4 : nae, I+ coeruleae.

Typus: Sri Lanka, Sabaragamuwa Province, Ratnapura District, Sinharaja Forest Reserve, Weddagala, 13 Feb. 1976, *M. E. Hale* 47 145 (US—holotypus; AMH, BM, PDA, isotypi).

Thallus greenish to whitish mineral gray, 8–12 cm broad, smooth to rugulose, continuous; cortex loosely organized and irregularly pored, *c.* 5 μm thick; algal layer continuous, 10 μm; medulla 10 μm; mostly hypophloeodal; apothecia conspicuous, strongly emergent with a more or less constricted base, 1·5–1·9 mm diam, the exciple carbonized; columella lacking; pore round to irregular, depressed at maturity, 0·2–0·4 mm diam, black rimmed; hymenium

210 μm; spores colourless, transversely septate, 12–22 × 80–155 μm, 24–27 loculate, 2–4/ascus, I+.

Chemistry. Hypoprotocetraric acid.

Habitat. Lower trunk to mid bole of trees in rain forest at lower to mid elevations (300–800 m).

Distribution. Sri Lanka.

Additional specimens. Hale collections: 2 (51 230), 4 (47 120, 47 146, 50 395).

Observations. I had at first identified this species with *O. pertusariiformis* but the chromatographic profiles differ, although apparently very closely related compounds are involved. Aside from the chemical difference, *O. neopertusariiformis* has a larger, depressed pore and a thinner, pored cortex. It also occurs at lower elevations, whereas rare *O. pertusariiformis* seems to be restricted to high elevations.

26. **Ocellularia nylanderiana** Hale in *Phytologia* **26** : 414 (1973).
(Fig. 18i)

Ascidium majorinum var. *longius* Nyl., *Sert. Lich. Trop. Labuan Singapore* : 20 (1891). Type: Singapore, 1879, *Almquist* s.n. (H-Nyl. 22 386—lectotype; S—isolectotype).
Icones. Hale, 1973 : 41 fig. 3.

Thallus whitish to ashy gray, 3–12 cm broad, shiny, becoming rugulose-verruculose; cortex loosely organized with irregular pores, 8–12 μm; algal layer continuous, 15 μm; medulla 10–15 μm, with crystals, mostly hypophloeodal; apothecia not abundant, strongly emergent, 1–1·5 mm diam, the amphithecium rugose, easily abraded to expose the underlying thick medulla, exciple heavily carbonized; columella 200–290 μm diam; pore irregular, 0·2–0·4 mm diam, sometimes faintly white rimmed; hymenium 100–240 μm; spores colourless, transversely septate, 10–20 × 90–180 μm, about 18 loculate 2/ascus, I+.

Chemistry. 'Chonestoma' unknowns (2 P− spots).

Habitat. Lower trunk into the canopy in rain forest at low elevations (100–300 m).

Distribution. Sri Lanka, Peninsular Malaysia, Philippines, Solomon Islands.

Additional specimens. Hale collections: 3a (46 317), 4 (47 096, 47 132, 47, 139, 50 474), 6 (47 188), 7a (50 096, 50 153), 7b (51 088, 51 095, 51 246, 51 256), 8 (47 021, 47 038, 47 044, 47 045), 9 (46 203).

Observations. I have placed under this name all columellate, 'chonestoma' unknown-containing species with large spores. The far commmoner *O. chonestoma* has much smaller spores, 18–30 μm long, but is otherwise externally very similar.

27. **Ocellularia orthomastia** (Krempelh.) Zahlbr., *Cat. Lich. Univers.* **2** : 597 (1923).
(Fig. 19a)

Ascidium orthomastium Krempelh. in *Nuovo G. bot. ital.* 7 : 60 (1875). Type: Singapore, *Beccari* 247 (M—lectotype; W—isolectotype).

Thallus greenish to whitish gray, 8–12 cm broad, shiny, smooth to verruculose, fissured; cortex rather thin and irregularly pored, 5 μm; algal layer 15–20 μm; medulla to 10 μm, with some crystals, mostly hypophloeodal; apothecia rather sparsely developed, semi-emergent to emergent, 0·8–1·1 mm diam, exciple carbonized; columella *c.* 190 μm diam; pore round to irregular, 0·3–0·4 mm diam, the tip of the columella visible within; hymenium 160 μm; spores colourless, transversely septate, 10 × 40–65 μm, 12–15 loculate, I+.

Chemistry. No substances present.

Habitat. Lower trunks to canopy in rain forest at low elevations (150 m).

Distribution. Sri Lanka, Malaya, Philippines, Sarawak, Sabah.

Additional specimens. Hale collections: 9 (46 142, 46 156, 46 192).

Observations. This is the first report of the species since its original publication in 1875. Krempelhuber could not find spores but cited measurements (7 × 52 μm) made by the sender, Dr Koch Onosbalci. Most apothecia in the type collections are indeed moribund, but I found a fertile one, confirming the measurements by Koch. The spores are I+ blue and 12–15 loculate.

28. Ocellularia papillata (Leighton) Zahlbr., *Cat. Lich. Univers.* **2** : 597 (1923). (Fig. 19b)

Thelotrema papillatum Leighton in *Trans. Linn. Soc. Lond.* **27** : 169 (1870). Type: Sri Lanka, Central Province, *Thwaites* C. L. 129 (BM—lectotype; H-Nyl. 3854, G, PC, PDA, S, UPS, W—isolectotypes).
Icones. Hale, 1974*a* : 23 fig. 12d (lectotype) and fig. 12e—Hale, 1978*a* : 27 fig. 7b.

Thallus whitish to light greenish gray, 3–12 cm broad, shiny, continuous, smooth to verruculose with age; cortex dense, 20–25 μm, with poorly developed aculeate hyphae, splitting somewhat internally; algal layer continuous, 10 μm; medulla to 10 μm, mostly hypophloeodal; apothecia common, immersed, sometimes slightly raised, 0·4–0·7 mm diam, the exciple becoming carbonized; columella variably developed, 20–210 μm, rarely lacking; pore round, 0·1–0·15 mm diam, becoming white rimmed; hymenium 80–160 μm; spores colourless, transversely septate, 4–6 × 12–28 μm, 5–6 loculate, I+.

Chemistry. No subsances present.

Habitat. Saplings, base to mid bole of trunks in rain forest at lower elevations (150–850 m).

Distribution. West Indies, Central and South America, India, Sri Lanka, Philippines, New Caledonia.

Additional specimens. Hale collections: 1 (50 224), 2 (51 107), 3a (46 288), 3b (46 390), 4 (47 101, 47 113, 47 163, 50 380, 50 390, 50 396, 50 419, 50 424, 50 427, 50 431, 50 435, 50 436, 50 437, 50 438, 50 445, 50 450, 50 451, 50 455, 50 460, 50 460A, 50 462, 50 471, 50 473), 7a (50 140, 50 171), 7b (50 309, 51 030, 51 062), 8 (47 004, 47 050), 9 (46 216). Thwaites collections: C. L. s.n. (PDA).

Observations. As in Panama (Hale 1978*a* : 26), this is one of the commonest species at base level in lower elevation rain forest. The columella varies considerably, from weakly if at all developed, to distinct. In general the Sri Lankan specimens only rarely have raised apothecia.

29. Ocellularia perforata (Leighton) Müll. Arg. in *Hedwigia* **31** : 284 (1892). (Fig. 19c)

Thelotrema perforatum Leighton in *Trans. Linn. Soc. Lond.* **25** : 447 (1886). Type: Brazil, Casiquiari, *Spruce* 254 (BM—lectotype; H-Nyl. 22557—isolectotype).
For additional synonymy see Hale, 1974*a* : 25.
Icones. Redinger, 1936 : 50 fig. 26.—Hale, 1974*a* : 23 fig. 12f (lectotype)—Hale 1978*a* : 37 fig. 7c.

Thallus pale yellowish to greenish gray, 8–10 cm broad, shiny, smooth to verruculose; cortex dense but rather thin, 5–7 μm, with weakly developed aculeate hyphae; algal layer continuous, 15 μm; medulla 10 μm or less, mostly hypophloeodal; apothecia numerous, immersed to barely semi-emergent, 0·2–0·4 mm diam, the exciple carbonized; columella 45–100 μm diam; pore round, 0·05–0·1 mm diam, often filled with tip of columella; hymenium 75–120 μm; spores colourless, transversely septate, 4–6 × 12–24 μm, 5–8 loculate, I+.

Chemistry. Protocetraric acid.

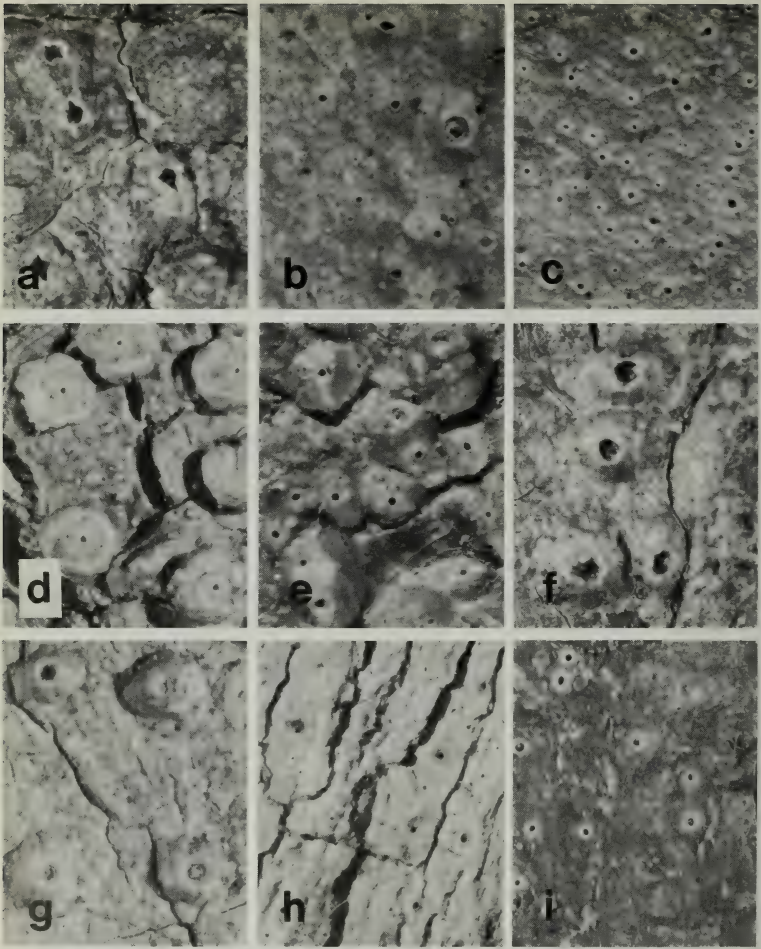

Fig. 19 Species of *Ocellularia*. (a) *O. orthomastia* (Hale 46 192). (b) *O. papillata* (Hale 445). (c) *O. perforata* (Hale 51 546). (d) *O. pertusariiformis* (Hale 50 274). (e) *O. pluripora* (Hale 51 168). (f) *O. polillensis* (Hale 50 510). (g) *O. punctulata* (Hale 51 243). (h) *O. pyrenuloides* (Hale 46 283). (i) *O. rassagala* (Hale 51 216). See Fig. 7i for scale.

HABITAT. Saplings and base of trees in rain forest at low to mid elevations (150–850 m).

DISTRIBUTION. West Indies, Central and South America, India, Sri Lanka, Java, Australia, Solomon Islands, Hawaii.

ADDITIONAL SPECIMENS. Hale collections: 1 (50 220), 2 (51 101), 3b (46 387), 4 (47 103, 51 112, 51 146, 51 159, 51 176, 51 182, 51 183), 7b (51 014, 51 028, 51 071), 8 (47 010).

OBSERVATIONS. *Ocellularia perforata* occupies the same habitats as *O. papillata* and is differentiated from it by the chemisty (P+ red) and the generally semi-emergent apothecia. It is much less common here than *O. papillata*; the reverse is true in the American tropics. When examining the Spruce type from South America, Redinger (1936 : 51) did not find a columella, but I was able to detect one in the BM material, rather weakly developed but definitely present.

30. **Ocellularia pertusariiformis** (Leighton) Zahlbr., *Cat. Lich. Univers.* **2** : 598 (1923).
(Fig. 19d)

Thelotrema pertusariaeforme Leighton in *Trans. Linn. Soc. Lond.* **27** : 170 (1870). Type: Sri Lanka, Central Province, *Thwaites* C. L. 97 (BM—lectotype; G, PC—isolectotypes).

Thallus whitish mineral gray, 3–5 cm broad, smooth to verruculose, continuous or fissured with age; cortex cellular, 7–10 μm, with some aculeate hyphae and internal splitting; algal layer continuous, 15 μm; medulla 10–60 μm with some crystals; apothecia conspicuous, emergent and basally constricted, warty, 1–1·4 mm diam, the exciple fused, reddish brown; columella lacking; pore area flattened to depressed, pore 0·05–0·08 mm diam, white rimmed; hymenium 300–450 μm; spores colourless, transversely septate, 28–33 × 105–135 μm, 11–12 loculate, 1–2/ascus, I+.

CHEMISTRY. Unidentified OP–1 and OP–2 (OP–1 near notatic acid and could be the depsidone of evernic acid—C. F. Culberson), both P−.

HABITAT. Twigs and lower trunk in high elevation rain forest (2100 m).

DISTRIBUTION. Sri Lanka.

ADDITIONAL SPECIMENS. Hale collections: 10 (50 274), 12 (50 342). Thwaites collections: C. L. 26 (BM, G, H-Nyl. 3922, PC, PDA), C. L. 257 (PDA) (as 'Lgt. 96, *Ascidium pertusariaeforme*') (some duplicates in BM and PDA include mixtures of *Myriotrema microstomum).*

OBSERVATIONS. This is a rare species occurring only at higher elevations. It is unknown outside of Sri Lanka. The closest relative is *O. neopertusariiformis* which has different chemistry and a more loosely organized cortex.

31. **Ocellularia pluripora** Hale **sp. nov.**
(Fig. 19e)

Thallus corticola, epiphloeodes, viridi-cinereus, 5–12 cm latus; apothecia semi-emergentia, solitaria vel aggregata, multicavata, 0·6–1·0 mm diametro, excipulo fuligineo, columella 90–130 μm diametro; ostiolum rotundatum, 0·05–0·1 mm diametro; hymenium 90–120 μm altum; sporae incolores, transversim septatae, octonae, 5–8 × 14–21 μm, 5–7 loculatae, I+ coeruleae.

Typus: Sri Lanka, Sabaragamuwa Province, Ratnapura District, Halwathura to Kanda, near Rassagala, elev. 900 m, 15 Mar. 1978, *M. E. Hale* 51 168 (US—holotypus; BM—isotypus).

Thallus dull greenish gray, 5–12 cm broad, shiny, continuous; cortex dense 10–12 μm, with aculeate hyphae, splitting internally; algal layer 15 μm, interrupted by crystals; medulla to 130 μm with remnants of cortical layers and large crystals; apothecia numerous, semi-emergent, solitary or fused with 2 or more pores in the same wart, 0·6–1·0 mm diam, the exciple weakly carbonized; columella 90–130 μm; pore round, 0·05–0·1 mm diam, white rimmed; hymenium 90–120 μm; spores colourless, transversely septate, 5–8 × 14–21 μm, 5–7 loculate, I+.

CHEMISTRY. Psoromic and norpsoromic acids.

HABITAT. Lower trunk into the canopy in rain forest at low to mid elevations (150–1000 m).

DISTRIBUTION. Sri Lanka.

ADDITIONAL SPECIMENS. Hale collections: 1 (50 207), 2 (51 133, 51 204), 3a (46 377), 4 (47 100, 47 143), 5 (46 225, 46 238), 8 (47 023), 9 (46 919, 46 200).

OBSERVATIONS. The diagnostic feature of this endemic species is the frequent occurrence of grouped or fused apothecia with 1–3 pores. The apothecia are significantly larger and more emergent than those of *O. terebrata* (Ach.) Müll. Arg., the only comparable species on the world level.

32. **Ocellularia polillensis** (Vainio) Hale **comb. nov.**
(Fig. 19f)

Thelotrema polillense Vainio in *Suom. Tiedeakat. Toim.* A, **15**(6) : 180 (1921). Type: Philippines, Polillo Island, Aug. 1909, *C. Robinson, Bur. Sci.* 9098 (TUR-Vain. 26 839—lectotype; FH—isolectotype).

Thallus greenish mineral gray, 6–15 cm broad, shiny, continuous or fissured; cortex dense, 10–13 μm, with aculeate hyphae, very little splitting internally; algal layer continuous, 15 μm; medulla 10–70 μm, with crystals; apothecia semi-emergent to emergent, 0·7–1·1 mm diam, exciple carbonized; columella entire but becoming more or less reticulate at maturity, 320–350 μm diam, the pruinose tip often filling the pore; pore gaping, 0·2–0·4 mm diam; hymenium 70–120 μm; spores colourless, muriform, 6–10 × 15–24 μm, 1–2 × 4–6 loculate, I+.

CHEMISTRY. Psoromic acid with or without norpsoromic acid.

HABITAT. Base and lower trunk of trees in rain forest at low to mid elevations (150–850 m).

DISTRIBUTION. Sri Lanka, New Caledonia, Philippines.

ADDITIONAL SPECIMENS. Hale collections: 2 (51 184), 3a (46 286, 46 287), 3b (46 383), 4 (47 137, 50 374, 50 465, 50 467, 50 508), 5 (46 226, 46 252), 6 (47 191), 7b (51 089), 8 (50 508), 9 (46 154).

OBSERVATIONS. This common species can be recognized by the gaping pore and reticulate columella. Externally it is close to *O. crassa,* which would be separated by the more erect, jagged thalline rim. The psoromic acid-containing species of *Ocellularia* often present taxonomic difficulties since they tend to intergrade. I am recognizing *O. polillensis* as the reticulate-columellate member of a columellate group that includes *O. asiatica* (Vainio) Hale, *O. straminea* (Vainio) Hale, and perhaps *O. leucina* (Müll Arg.) Hale, all of which have a simple columella.

33. **Ocellularia punctulata** (Leighton) Zahlbr., *Cat. Lich. Univers.* **2** : 599 (1923).
(Fig. 19g)

Ascidium punctulatum Leighton in *Trans. Linn. Soc. Lond.* **27** : 171 (1870). Type: Sri Lanka, Central Province, *Thwaites* C. L. 127 (BM—lectotype; G, PC, PDA—isolectotypes).

Thallus light yellowish to greenish gray, 2–8 cm broad, smooth to finely verruculose, fissured with age; cortex thin with irregular pores, 5 μm, with some aculeate hyphae; algal layer 10 μm; medulla variable 10–30 μm, more or less uniformly orange, with numerous crystals; apothecia numerous, emergent, 0·8–1·0 mm diam, the exciple carbonized; columella 70–240 μm, protruding into the pore; pore round, somewhat depressed, 0·1–0·2 mm diam; hymenium 80–115 μm; spores colourless, transversely septate, 5–6 × 15–30 μm, 6–10 loculate, I+.

CHEMISTRY. 'Cinchonarum' unknowns (P+ red) an an unidentified K+ purplish pigment.

HABITAT. Base and lower trunk and saplings in rain forest at low to mid elevations (150–850 m).

DISTRIBUTION. Sri Lanka.

ADDITIONAL SPECIMENS. Hale collections: 1 (50 201, 50 212, 50 251), 2 (51 123, 51 191, 51 197), 3a (46 367, 46 374), 4 (47 070, 47 088, 47 118, 47 122, 50 406, 50 433, 50 440, 50 452, 50 461, 50 517), 6 (47 170), 7a (50 149, 50 181, 50 185), 7b (50 308, 51 010, 51 041, 51 048, 51 064, 51 091, 51 243), 8 (47 013, 47 017, 47 019, 47 047), 9 (46 153, 46 178).

OBSERVATIONS. This is one of the most unusual Sri Lankan endemics, widely distributed in the lowland rain forest. The pigmented medulla was not noticed by Leighton. On the world level it is a close relative of *O. cavata* (Ach.) Müll Arg., which has a white or pale yellowish, K– medulla and spores generally more than 30 μm long (Hale, 1978*a* : 16). They have the same P+ red chemistry.

The epithet '*punctulatum*' has been a source of confusion ever since Leighton published the species. Zahlbruckner (1923 : 599) listed it as '*pustulata*', an obvious slip. Leighton had sent it to Nylander for comment in 1868 labelled '*Ascidium punctulatum*',. Nylander (in litt. 27 June 1868) identified it as '*Thelotrema punctulatum* Nyl. Lich. Extot. 222' except that the spores were not brown. In the Nylander herbarium at Helsinki I found a specimen labelled '*Thelotrema punctulatum* Nly., Ins. Cubae, 22446. "Th. 25" ', which can be identified as *Myriotrema compunctum*. This identification was apparently never published. Nylander had, however, already published the epithet without a description in his *Conspectus generis Thelotrematis* (1862 : 96) as '27. *Th punctulatum* Nyl. (*Por. compunctum* Ach.).—Amer.' The specimen on which this name was based is Nyl.-herb. 22691, which is also *Myriotrema compunctum* Ach., which is, according to Salisbury (1978 : 414), *Thelotrema sordidescens* (Fée) Nyl. At the same time Salisbury lists in synonymy an '*Ascidium punctulatum* (Nyl.) Kremph.', but in his monograph of *Ascidium* Krempelhuber (1877 : 132) cited '*Ascidium punctulatum* Leight.' and does not refer to the Nylander epithet. In any event the combination *Ocellularia punctulata* appears to be valid.

34. Ocellularia pyrenuloides Zahlbr. in Magnusson & Zahlbr. in *Ark. Bot.* **31A**(1) : 46 (1944).
(Fig. 19h)

Type: Hawaii, Wailuku, *Faurie* 676 (W—lectotype).
ICONES. Hale, 1974*a* : 23 fig. 12j (lectotype) and fig. 12k.

Thallus whitish gray, 8–12 cm broad, shiny, continuous; cortex poorly developed and in large part lacking; algal layer scattered among superficial medullary hyphae or hypophloeodal, to 15 μm; medulla mostly hypophloeodal; apothecia immersed in periderm, inconspicuous, 0·3 mm diam, the exciple carbonized apically; columella 60–90 μm; pore round, 0·6–0·9 mm diam, usually darkening; hymenium 40–45 μm; spores colourless, transversely septate, 5–6 × 15–18 μm, 4–6 loculate, I+.

CHEMISTRY. Stictic acid with or without constictic acid.

HABITAT. Lower trunk in rain forest at low to mid elevations (300–1100 m).

DISTRIBUTION. West Indies, Venezuela, Hawaii, Sri Lanka.

ADDITIONAL SPECIMENS. Hale collections: 4 (50 448), 5 (46 283).

OBSERVATIONS. I had earlier identified this lichen from Dominica in the West Indies (Hale, 1974*a* : 25) and it now appears to be pantropical. The blackening of the pore was described by Zahlbruckner as 'circum discum nigro-annulatae'. This is caused by exposure of the exciple but can be variable with thalline tissue sometimes masking the rim completely. The diagnostic characters would have to be lack of a cortex and presence of a columella and stictic acid. A very close relative, *O. tenuis* (below), has somewhat larger, muriform spores which are negative with iodine.

35. **Ocellularia rassagala** Hale **sp. nov.**
(Fig. 19i)

Thallus corticola, epiphloeodes, nitidus, continuus, cinereo-viridis, *c.* 10 cm latus; apothecia immersa, 0·3–0·4 mm diametro, excipulo fuligineo, columella *c.* 60 μm diametro; ostiolum rotundatum, 0·1 mm diametro, albo-cinctum; hymenium 120–150 μm altum; sporae fuscae, transversim septatae, octonae, 6–/ × 14–18 μm, 5–6 loculatae, I–.

Typus: Sri Lanka, Sabaragamuwa Province, Ratnapura District, Halwathura-Kanda, near Rassagala, elev. 850 m, 15 Mar. 1978, *M. E. Hale* 51 216 (US—holotypus; BM—isotypus).

Thallus greenish mineral gray, *c.* 10 cm broad, shiny, continuous; cortex 20–30 μm, with aculeate hyphae, splitting and exfoliating; algal layer continuous, 15 μm; medulla to 30 μm, with crystals; apothecia immersed in the periderm, 0·3–0·4 mm diam, slightly raised at maturity, the exciple carbonized; columella *c.* 60 μm diam; pore round, 0·1 mm diam, white rimmed; hymenium 120–150 μm; spores brown, transversely septate, 6–7 × 14–18 μm, 5–6 loculate, I–.

CHEMISTRY. Psoromic acid.

HABITAT. Trees along trail at mid elevations (850 m).

DISTRIBUTION. Sri Lanka.

OBSERVATIONS. A rather inconspicuous species, *O. rassagala* can be distinguished from other brown-spored members of *Ocellularia* because of the immersed columellate apothecia and chemistry.

36. **Ocellularia rhicnopora** Hale **sp. nov.**
(Fig. 20a)

Thallus corticola, epiphloeodes, verrucosus vel fere granulosus, albido-cinereus, 15 cm latus; apothecia numerosa, irregulariter dispersa, semi-emergentia, amphithecio pallide brunneo, 0·7–1·0 mm diametro, excipulo connato, columella nulla; ostiolum 0·1–0·2 mm diametro, nigro-cinctum; hymenium *c.* 90 μm altum; sporae incolores, transversim septatae, octonae, 8 × 30 μm, 7–9 loculatae, I+ coeruleae.

Typus: Sri Lanka, Southern Province, Galle District, Kanneliya Forest Reserve, elev. 150 m, 16 Feb. 1976, *M. E. Hale* 46 147 (US—holotypus: BM—isotypus).

Thallus pale yellowish brown to whitish, *c.* 15 cm broad, finely verruculose to subgranular; cortex loosely organized, 20–24 μm; algal layer continuous, 15 μm; medulla to 20 μm but mostly hypophloeodal; apothecia irregularly dispersed, semi-emergent, 0·7–1·0 mm diam, the exciple carbonized; columella lacking; pore irregular, 0·1–0·2 mm diam, the surrounding area pale brown, rugose; hymenium *c.* 90 μm; spores colourless, transversely septate, 8 × 30 μm, 7–9 loculate, I+.

CHEMISTRY. No substances present.

HABITAT. Lower trunk in rain forest at low elevations (150 m).

DISTRIBUTION. Sri Lanka.

ADDITIONAL SPECIMENS. Hale collections: 5 (46 246, 46 254).

OBSERVATIONS. This species is apparently near the hypoprotocetraric acid-containing, ecolumellate, *O. domingensis* group, which in Sri Lanka includes *O. kanneliyensis* and *O. neopertusariiformis*. They all have large, emergent apothecia with a carbonized exciple, a rather loosely organized cellular cortex, and no aculeate hyphae or splitting. *Ocellularia rhicnopora* has an unusually broad, wrinkled pore area set off from the main thallus by the pale brown colour.

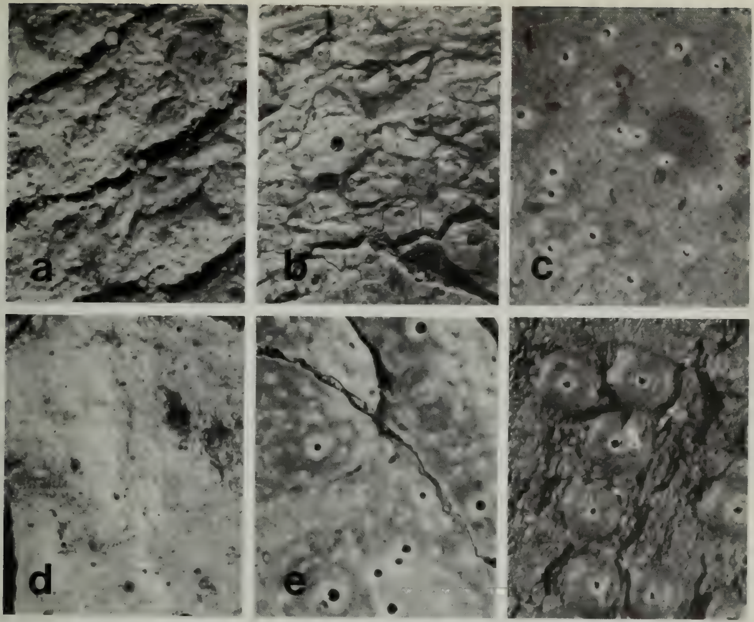

Fig. 20 Species of *Ocellularia*. (a) *O. rhicnopora* (Hale 46 147). (b) *O. sticticans* (Hale 46 254). (c) *O. subsimilis* (Hale 51 141). (d) *O. tenuis* (Hale 46 267). (e) *O. thelotremoides* (Hale 51 040). (f) *O. triglyphica* (Hale 51 194). See Fig. 7i for scale.

37. **Ocellularia sticticans** Hale **sp. nov.**

(Fig. 20b)

Thallus corticola, epiphloeodes, continuus, nitidus, 15 cm latus; apothecia vix emergentia, 0·4–0·7 mm diametro, excipulo fuligineo, columella 45–50 μm diametro; hymenium 35–40 μm altum; sporae incolores, transversim septatae, octonae, 5–8 × 12–30 μm, 6–8 loculate, I+ coeruleae.

Typus: Sri Lanka, Southern Province, Matara District, Enselwatta, elev. 1100 m, 14 Feb. 1976, *M. E. Hale* 46 254 (US—holotypus; BM—isotypus).

Thallus ashy white, *c.* 15 cm broad, thin but continuous, shiny; cortex dense, 12–20 μm; algal layer continuous, 10–15 μm; medulla to 30 μm; apothecia weakly emergent, 0·4–0·7 mm diam, the exciple carbonized; columella 40–50 μm, protruding into the pore; hymenium 35–40 μm; spores colourless, transversely septate, 5–8 × 12–30 μm, 6–8 loculate, I+.

CHEMISTRY. Stictic acid.

HABITAT. Lower trunks and sapling in rain forest at low to mid elevations (300–1100 m).

DISTRIBUTION. Sri Lanka, Solomon Islands.

ADDITIONAL SPECIMENS. Hale collections: 5 (46 246), 7a (50 158). Other collections: Solomon Islands: Kolombangara Island, *Hill* 10 654 (BM, US); Santa Isabel Island, *Hill* 11 249 (BM, US).

OBSERVATIONS. One would probably identify this species as *O. perforata* without using a chemical test. Aside from the chemical difference, it has more consistently emergent apothecia.

38. **Ocellularia subsimilis** (Hale) Hale in *Mycotaxon* **11** : 138 (1980).
(Fig. 20c)

Thelotrema subsimile Hale in *Phytologia* **27** : 497 (1974). Type: Trinidad, Arima, 17 April 1972, *M. E. Hale* 37 447 (US—holotype).
ICONES. Hale, 1974*b* : 501 fig 17.

Thallus whitish gray, 6–10 cm broad, shiny, smooth, continuous; cortex dense, 8–15 μm, with aculeate hyphae and some internal splitting; algal layer continuous, 10–15 μm; medulla 0–60 μm, with some crystals; apothecia immersed to slightly raised, 0·5–0·8 mm diam, the exciple carbonized; columella *c.* 60 μm diam; pore round, 0·05–0·1 mm diam, the tip of the columella usually visible within; hymenium 120–150 μm; spores colourless, muriform, 6–10 × 22–30 μm, 1–3 × 5–6 loculate, I+.

CHEMISTRY. Protocetraric acid.

HABITAT. On trees along trails occurring into the canopy branches in rain forest in a broad range of elevations (150–2100 m).

DISTRIBUTION. West Indies, India, Sri Lanka, Philippines.

ADDITIONAL SPECIMENS. Hale collections: 2 (51 141), 9 (46 134), 11 (50 317). Thwaites collections: C. L. 118 (BM, H-Nyl. 3866, PDA, UPS) (as 'Lgt. 80. *T. calvescens*').

OBSERVATIONS. This species is externally identical with *O. perforata,* the main difference being the muriform spores. Leighton's determination of C. L. 118 as '*Thelotrema calvescens*' (= *Myriotrema calvescens* (Fée) Hale) may have been suggested and was at least confirmed by Nylander. Fée's type contains psoromic acid and has transversely septate spores (see Hale, 1978*a* : 15 and Salisbury, 1978 : 416).

39. **Ocellularia tenuis** (Hale) Hale in *Mycotaxon* **11** : 138 (1980).
(Fig. 20d)

Thelotrema tenue Hale in *Smithson. Contr. Bot.* **16** : 38 (1974). Type: Dominica, Morne Diablotin, Jan. 1969, *M. E. Hale* 35 430 (US—holotype).
ICONES. Hale, 1974*a* : 37 fig. 17k (holotype).—Hale, 1978*a* : 46 fig. 13j.

Thallus whitish mineral gray, 3–6 cm broad, shiny, thin, continuous; cortex lacking or very weakly developed as a thin polysaccharide layer with aculeate hyphae; algal layer 10 μm; medulla mostly hypophloeodal; apothecia immersed, 0·2–0·3 mm diam, the exciple weakly carbonized; columella 30–50 μm diam, sometimes lacking; pore round, 0·05 mm diam, becoming black rimmed; hymenium 70–90 μm; spores colourless, muriform 8–10 × 26–28 μm, 2 × 6–7 loculate, I–.

CHEMISTRY. No substances present.

HABITAT. Trees along trail in mossy forest at mid elevations (1100 m).

DISTRIBUTION. West Indies, Central and South America, Sri Lanka.

ADDITIONAL SPECIMENS. Hale collections: 5 (46 267).

OBSERVATIONS. *Ocellularia tenuis* is obviously related to *O. melanotremata,* which contains stictic acid (see above), because of the black-rimmed pore and ecorticate thallus.

40. Ocellularia thelotremoides (Leighton) Zahlbr., *Cat. Lich. Univers.* **2** : 603 (1923). (Fig. 20e)

Ascidium thelotremoides Leighton in *Trans. Linn. Soc. Lond.* **27** : 170 (1870). Type: Sri Lanka, Central Province, *Thwaites* C. L. 142 (BM—lectotype; G, H-Nyl. 3920, PC, S, UPS, W—isolectotypes) (as 'Lgt. 97. *Ascidium thelotremoides*') (C. L. 256 so determined in PDA is a pyrenocarpous lichen).

Thallus pale greenish to straw coloured, 8–15 cm broad, shiny, continuous, slightly rugulose and white spotted with age; cortex dense, rather thin, 8–10 μm; algal layer continuous, 12–15 μm; medulla 10–45 μm, with crystals; apothecia immersed to slightly raised, 0·3–0·6 mm diam, the exciple carbonized; columella *c.* 90 μm diam or sometimes lacking; pore round, 0·1–0·2 mm diam; hymenium 95–150 μm; spores colourless, muriform, 6–10 × 18–30 μm, 1–2 × 5–9 loculate, I+.

CHEMISTRY. Fumarprotocetraric and protocetraric acids.

HABITAT. Exposed roots, saplings, and base and lower trunk of trees in rain forest at low to mid elevations (150–850 m).

DISTRIBUTION. India, Sri Lanka, Philippines.

ADDITIONAL SPECIMENS. Hale collections: 1 (50 194, 50 196, 50 245, 50 259), 2 (51 115, 51 174, 51 186, 51 198), 3b (46 388), 4 (50 379, 50 403, 50 423, 50 501, 50 502), 7b (51 002, 51 019, 51 040, 51 074, 51 076), 8 (47 016, 47 030, 47 049, 47 051).

OBSERVATIONS. This species often occurs with *O. papillata* and *O. perforata,* both of which resemble it externally but have transversely septate spores. I confirmed the chemistry of all collections with both hexane-ether-formic acid and n-butanol-acetone-water solvent systems.

41. Ocellularia triglyphica (Krempelh.) v. Overeem & D. v. Overeem in *Bull. Jard. bot. Buitenz.* III, **4** : 119 (1922). (Fig. 20f)

Ascidium triglyphicum Krempelh. in *Nuovo G. bot. ital.* **7** : 22 (1875). Type: Sarawak, *Beccari* 129b (M—lectotype).
Ascidium melanostomum Krempelh. in *Flora, Jena* **59** : 248 (1876). Type: Brazil, Prov. Rio de Janeiro, *Glaziou* 5573 (M—lectotype; BM, G, PC, W—isolectotypes).
Ascidium majorinum Nyl., *Sert. Lich. Trop. Labuan Singapore* : 20 (1891). Type: Singapore, 1879, *Almquist* s.n. (H-Nyl. 22 387—lectotype; S—isolectotype).
Phaeotrema melanostomum (Krempelh.) Müll. Arg. in *J. Linn. Soc.* (Bot.) **30** : 454 (1895).
Ocellularia majorina (Nyl.) Zahlbr., *Cat. Lich. Univers.* **2** : 595 (1923).

Thallus pale greenish mineral gray, 5–12 cm broad, shiny, smooth to verruculose with age; cortex cellular, 10–15 μm; algal layer 10 μm; medulla 5–60 μm, with crystals, mostly hypophloeodal; apothecia conspicuous, strongly emergent, the base sometimes constricted, 0·8–1·1 mm diam, the exciple carbonized; columella 120–160 μm; pore round to irregular, 0·1–0·2 mm diam; white rimmed; hymenium 160–180 μm; spores colourless, transversely septate, 10–15 × 70–150 µm, 18–20 loculate, I+.

CHEMISTRY. Hypoprotocetraric acid, 4-O-demethylnotatic acid, and unknowns GU 1 and 2 (fide C. F. Culberson).

HABITAT. Base and lower trunks of trees in rain forest at mid or lower elevations (300–850 m).

DISTRIBUTION. South America, Sri Lanka, Peninsular Malaysia, Philippines, Sarawak.

ADDITIONAL SPECIMENS. Hale collections: 2 (51 187, 51 194, 51 202); 4 (50 411, 50 458, 50 467, 50 478), 7b (51 004).

Observations. This conspicuous lichen has an extensive synonymy. Dr C. F. Culberson kindly established the identity of the chemistry in the types of *Ascidium triglyphicum* and *A. majorinum.* Other columellate hypoprotocetraric acid-containing species on the world level include *O. phaeotropa* (Krempelh.) Müll. Arg., which has small spores (6 × 19 μm), and two large spored species, *O. granulifera* (Krempelh.) Müll Arg. with a coarsely granular thallus and *O. henatomma* (Ach.) Müll. Arg. with a smoother thallus and small pore (see Hale, 1972 : 192). Among the muriform spored species we can find *O. arecae* (Vainio) Hale, which has the same chemistry as *O. triglyphica,* and *O. grandis* (Hale) Hale, which has a strongly annulate pore and very large spores. The chemistry of these species is discussed in more detail by Culberson & Hale (1973).

Redinger (1936 : 26) considered *Ascidium melanostomum* to be a synonym of *Ocellularia rhabdospora* (Nyl.) Redinger, but that species, known only from the New World, contains the P+ red 'cinchonarum' unknown (Hale, 1978*a* : 29).

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Vascular plant collections from the Tristan da Cunha group of islands

Eric W. Groves

Department of Botany, British Museum (Natural History), Cromwell Road, London SW7 5BD

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Synopsis

An account of the collections of flowering plants and ferns made on the Tristan da Cunha group of islands is presented. A brief historical and topographical summary of each island is followed with a chronological and an alphabetical list of persons, expeditions and ships that have visited and collected vascular plants on the group. The systematic list gives details of the 212 vascular plant taxa recorded, which consists of 177 spermatophyte taxa (including 58 natives, of which 34 are endemic, and 119 aliens) and 35 pteridophyte taxa (all native including 20 endemics). Included are the descriptions of one new genus *Parodiochloa*, ten new species *(Agrostis goughensis, A. holgateana, A. trachychlaena, A. wacei, Calamagrostis deschampsiiformis, Deschampsia christophersenii, D. mejlandii, D. robusta, D. wacei, and Glyceria insularis)* one new sub-species *(Agrostis magellanica* subsp. *laeviuscula)*, and two new combinations *(Parodiochloa flabellata* and *Polypogon mollis*). All belong to the family Gramineae and are provided by C. E. Hubbard, with the exception of *Polypogon mollis* which is made in conjunction with the present author.

Introduction

Under each of the 212 vascular plants enumerated is given the scientific name and a brief relevant synonymy, the island vernacular name (where known), status, first known record, and habitat details. These last are a synthesis of the notes from collectors' labels. Inclusion of full data from every sheet would have made the text unnecessarily long, so data relating to all cited specimens have been recorded and stored in the data-bank associated with the British Antarctic Survey's bryophyte herbarium housed at the Research Station, Institute of Terrestrial Ecology, Bush Estate, Penicuik, Midlothian, Scotland.

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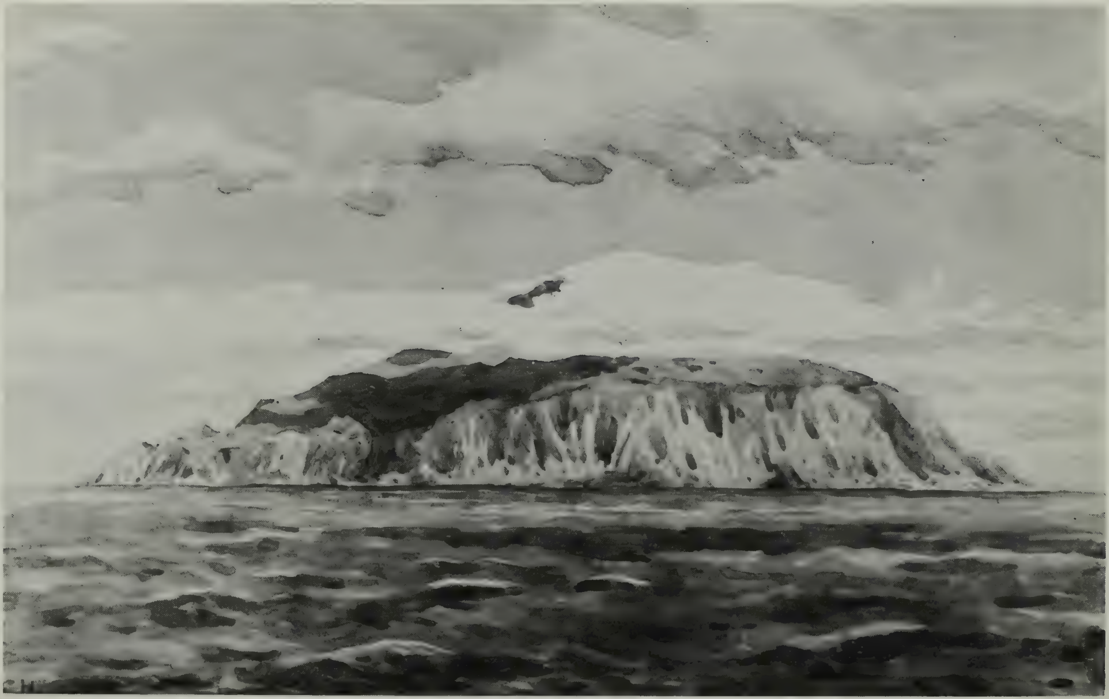

Fig. 1 Tristan da Cunha, viewed from the sea at about 3 km distance. Low cloud covers the Peak (2058 m). January 1926. From an original watercolour by Sir Alister Hardy.

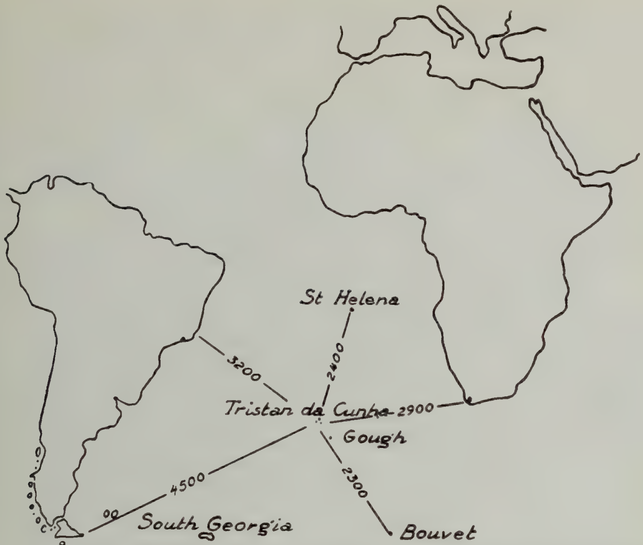

Fig. 2 Map showing the position of the Tristan da Cunha islands in the south Atlantic and their relative distance (in km) from adjacent continents and islands.

Following the habitat details is a citation of those herbarium specimens which have been examined by the author, indicated by collectors' names and numbers, together with abbreviations of the herbaria where such material is at present located. The citation of these abbrevations are given in order of the size and importance of the sets held. Thus, the first herbarium mentioned has the major set that contains the specimen in question; those following hold smaller sets. Institution abbreviations follow *Index Herbariorum* (Holmgren & Keuken, 1974) (see also pages 346 & 414).

This contribution represents the first listing of all available collections to date of vascular plants from the Tristan da Cunha group. Some may now possibly be extinct. Together with the earliest record for each species it forms a basic source work against which all future collections can be evaluated. Unfortunately I have been unable to make a personal visit to the islands.

History and topographical description

General

The Tristan da Cunha islands (including Gough Island) are an isolated group situated in the middle of the South Atlantic Ocean approximately mid-way between South Africa and South America (Fig. 2). They lie approximately 2400 km south of St Helena and 6440 km from the Antarctic continent. The 'Tristan-Gough group' as interpreted throughout this paper includes not only a cluster of five main islands: Tristan da Cunha, Inaccessible, Nightingale, Middle and Stoltenhoff, but also Gough Island which lies approx. 352 km further to the south- south-east and forms a natural member of the group (Fig. 3). The

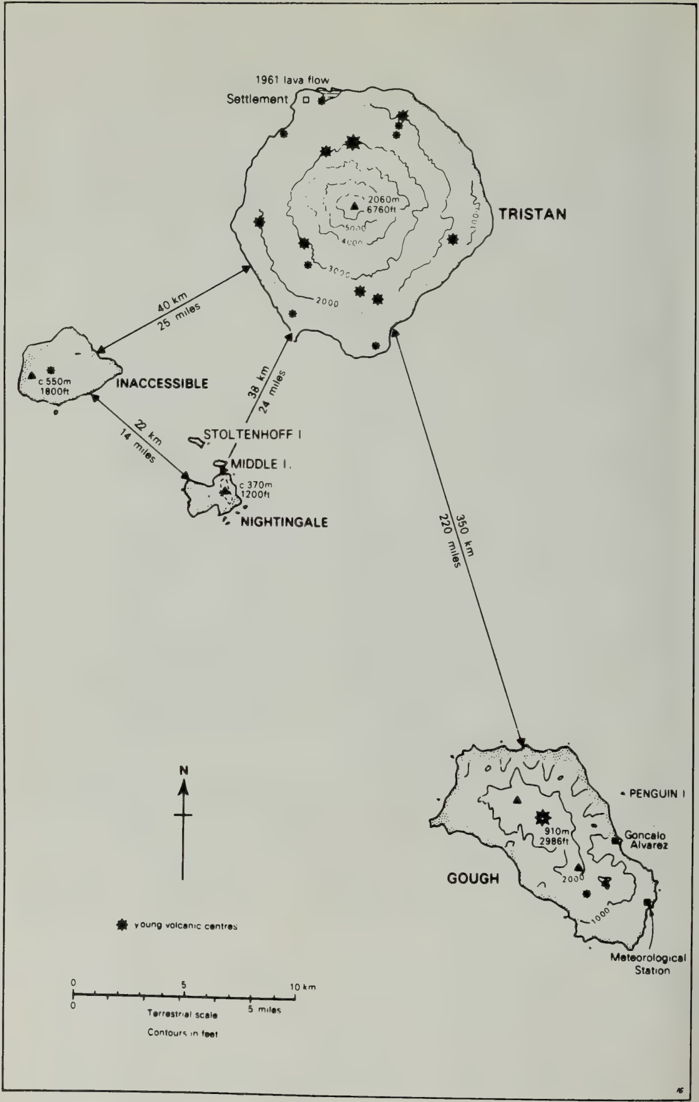
1961 lava flow
Settlement
2060m
6760ft
5000
4000
3000
2000
1000
TRISTAN
40 km
25 miles
c 550m
1800ft
INACCESSIBLE
38 km
24 miles
22 km
14 miles
STOLTENHOFF I
MIDDLE I.
c 370m
1200ft
NIGHTINGALE
350 km
220 miles
N
PENGUIN I
910m
2986ft
Goncalo Alvarez
GOUGH
2000
1000
Meteorological Station
young volcanic centres
0
5
10 km
0
5 miles
Terrestrial scale
Contours in feet

Fig. 3 Map showing the Tristan da Cunha group and distances between the major islands.

islands fall within an overall mean latitude and longitude of 37°S. 12°W., but the co-ordinates for the individual islands, taken either from the Admiralty Chart or from the South Atlantic Pilot, are as follows:

Tristan da Cunha	37° 06′ S.	12° 17′ W.
Inaccessible	37° 16′ S.	12° 52′ W.
Nightingale	37° 28′ S.	12° 32′ W.
Middle	37° 23′ 30″ S.	12° 28′ 30″ W.
Stoltenhoff	37° 23′ S.	12° 29′ W.
Gough	40° 19′ S.	9° 57′ W.

The islands are entirely volcanic in origin and are thought to have arisen from a series of isolated eruptions in mid-ocean. Geologically they are on the line of the mid-Atlantic ridge and are believed to have been formed during the Tertiary period. The geology of the group has been described in some detail by Dunne (1941).

The climate of the islands is temperate and of the extreme oceanic type, the prevailing winds being westerly. The air temperature is around 11–12°C throughout the year, and the mean annual rainfall, from such figures as are available, is 1656 mm for Tristan da Cunha (at the Settlement) and 3225 mm for Gough Island. It must be observed, however, that on Tristan da Cunha, where the Peak dominates the topography of the island, the rainfall consequently varies with position and altitude. Precipitation is greater on the western side of the island than on the east, and the rainfall on the Base and at the Peak is approximately one-and-a-half times and three times greater respectively than that around the Settlement (Wace & Holdgate, 1958: 595; Wace, 1961: 339).

Sealers and whalers, both British and American, made the Tristan group the centre for their activities from the middle of the 18th century, with the result that many of the place names commemorate either their ships or the men who served in them. A comprehensive list of these place names is given for Tristan by Crawford (1941: 219–228). A good map in Booy (1957: 8–9) indicates them; for Gough Island the map in Holdgate (1958: 211–216) should be consulted.

Tristan da Cunha

Tristan da Cunha (Fig. 4) was uninhabited by man when it was first discovered in 1506 by a Portuguese admiral named Tristao da Cunha. This island, with less than 100 sq km of land surface, is the largest of the Tristan-Gough group. The main area which is a volcano, some 13 km across and roughly octagonal in shape, is known as the Peak (2058 m). It rises to a gigantic cinder cone (Fig. 1) from about 1220 m up to the rim of the crater (now filled by a lake). The slopes below are deeply furrowed with ravines radiating out from the cone like the spokes of a wheel, and are covered with a dense vegetation of the tree fern *Blechnum palmiforme*. These slopes level out at the foot to a plateau which the islanders refer to as the Base, although this is still at altitudes at 240–610 m above sea-level. This plain is variously covered with grass sward merging into a scrub of *Phylica arborea* covered with moss. The vegetation of the island has been well described by Wace & Holdgate (1958). The island has been continuously inhabited (Fig. 5) since 1810, apart from the 18-month break following the eruption of 1961, with cottages built upon part of the larva plain along the north-west side, in an area referred to as the Settlement. Vegetables, mainly potatoes, are cultivated nearby in the Potato Patches (Fig. 6) and cattle are grazed on the adjacent slopes.

Inaccessible Island

Inaccessible Island (Fig. 7), next in size to Tristan da Cunha and lying about 32 km to the south-west, was so named by Captain d'Etchevery of the French ship *Etoile du Martin*. Having in 1778 successfully set foot on both Tristan da Cunha and Nightingale Islands, d'Etchevery came to a third island but, failing to find a suitable landing place, he recorded

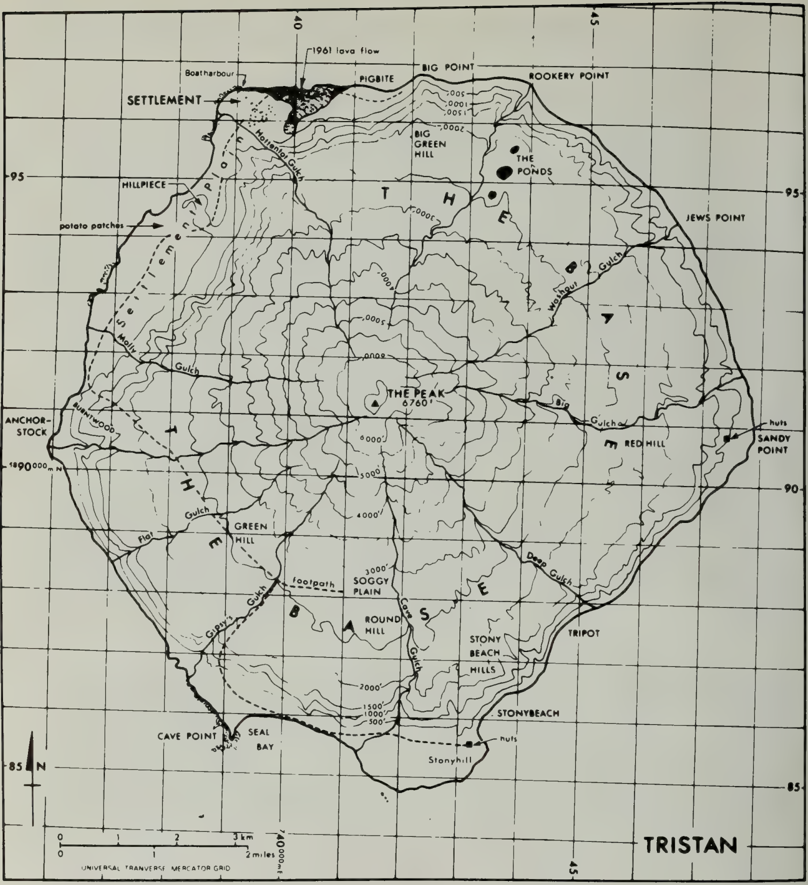
1961 lava flow
Boatharbour
SETTLEMENT
PIGBITE
BIG POINT
ROOKERY POINT
BIG GREEN HILL
THE PONDS
HILLPIECE
potato patches
Settlement Plain
Hottentot Gulch
THE BASE
JEWS POINT
Washout Gulch
Molly Gulch
THE PEAK 6760'
Big Gulch
RED HILL
ANCHOR-STOCK
Burntwood
huts
SANDY POINT
3890000mN
Flat Gulch
GREEN HILL
Deep Gulch
footpath
3000'
SOGGY PLAIN
ROUND HILL
Cave Gulch
Gipsy's Gulch
STONY BEACH HILLS
TRIPOT
STONYBEACH
CAVE POINT
SEAL BAY
huts
Stonyhill
2000'
1500'
1000'
500'
4000'
5000'
6000'
N
0 1 2 3 km
0 1 2 miles
UNIVERSAL TRANVERSE MERCATOR GRID
740000mE
40
45
95
90
85
TRISTAN

Fig. 4 Map of Tristan da Cunha.

his failure to posterity by giving that island what he thought was the well-deserved name of Inaccessible. Landings have subsequently proved possible by using a beach along the north-east shore, although not without some degree of difficulty. The island is pear-shaped in general outline, being about 4.8 x 4 km, with a truncated volcanic cone rising to 560 m on the south-west side, and with a flattened plateau in the centre. Around the island precipitous cliffs drop sheer to the sea, but above, and rising to the peak, the plateau is variously covered with tall tussock grass *(Spartina arundinacea),* a scrub of the tree-fern *(Blechnum palmiforme)* and small areas of stunted *Phylica arborea.* A spectacular waterfall, several kilometres high, cascades from one of the perpendicular cliffs down to Salt Beach below (Fig. 8). Inaccessible

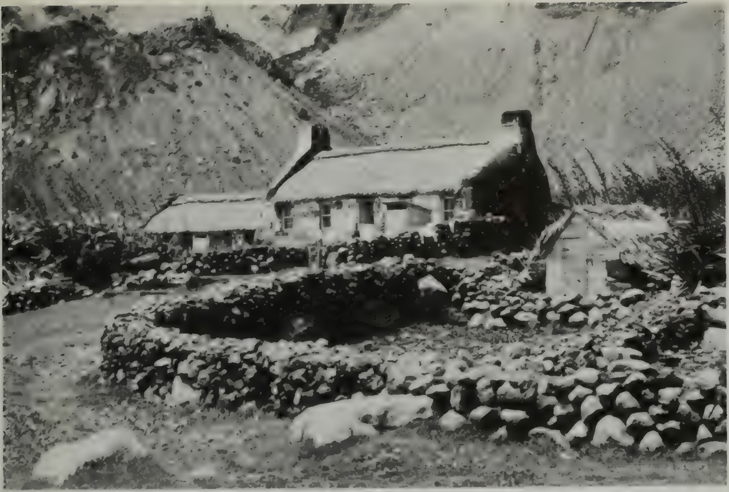

Fig. 5 David Hagen's house on Tristan da Cunha, one of the oldest on the island. Note clumps of New Zealand flax, *Phormium tenax*, planted within the stone walls to act as wind-breaks. October 1966. Photograph: George Edwards.

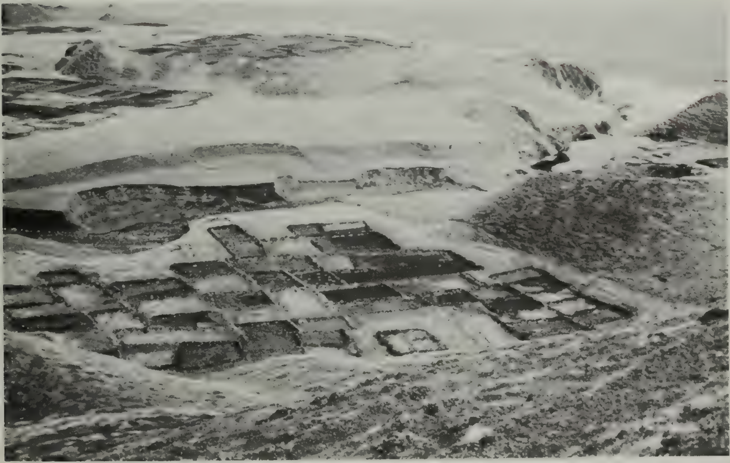

Fig. 6 The Potato Patches viewed from above on Hillpiece, Tristan da Cunha, and looking toward the western coastline of the island. October 1966. Photograph: George Edwards.

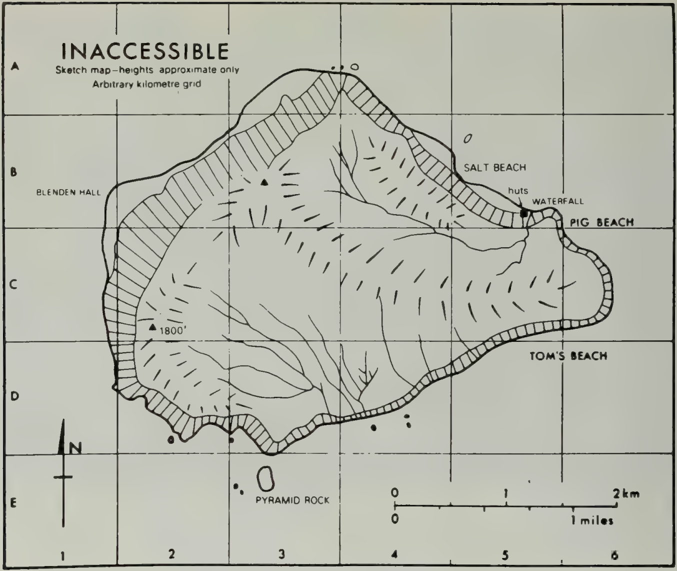

Fig. 7 Map of Inaccessible Island.

Island is the only known locality in the world for the flightless rail (*Atlantisia rogersi*) or 'Island hen' as named by the Tristan islanders (Green, 1973: 92), to distinguish it from a slightly larger bird formerly known on Tristan da Cunha itself called 'Island cock' (=Tristan moorhen) (*Gallinula nesiotis nesiotis*)—now unfortunately extinct.

Nightingale Island

Nightingale Island (Fig. 9) lying to the south-east of Inaccessible Island, and some 29 km south-south-west of Tristan da Cunha, is named after a British Naval Officer, Captain Gamaliel Nightingale, who visited the Tristan group in 1760. It is rectangular in shape, being about 1.6 km west to east and 1.2 km north to south. It has two peaks; the eastern one, more precipitous and conical, rises to 336 m, while the southern one reaches 292 m and has more gently sloping sides except on its southern flank. High cliffs bound its southern, eastern and western shores. The lower land and all but the steeper slopes are covered, as on Inaccessible Island, with tussock *(Spartina arundinacea),* the tree-fern *Blechnum palmiforme* and occasional thick patches of *Phylica arborea.* Moseley (1879: 108–109) described his difficulty in penetrating this vegetation and how he found that one large area, densely overgrown, had become a vast penguin rookery. It has been estimated that about two million pairs of the great shearwater (*Puffinus gravis*) nest in burrows on Nightingale Island (Rowan, 1952; Baird, 1965) and, together with those on Inaccessible and Gough Islands, form much the largest breeding colony for this species in the world.

Middle Island

Middle Island (Fig. 9) is situated less than 0.8 km north of Nightingale and is only about 0.4 km square in size. It is low lying and flat-topped, the highest point being only 45 m.

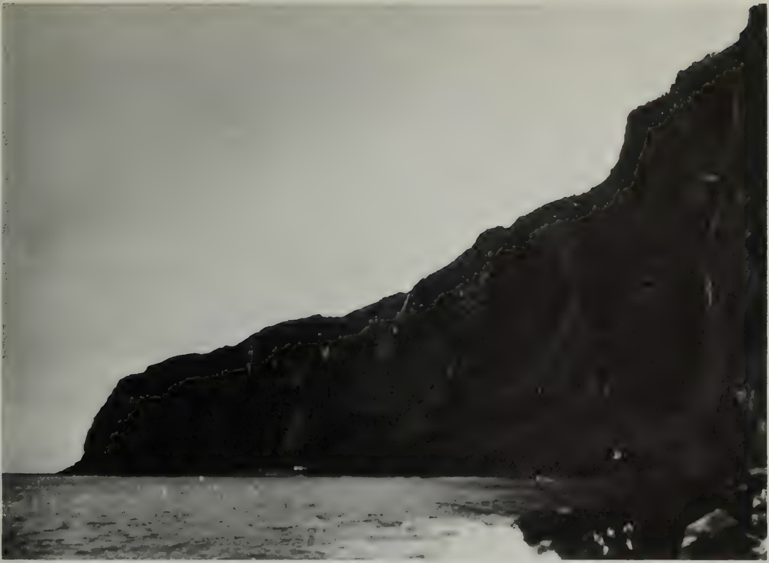

Fig. 8 Salt beach, Inaccessible Island, with cliffs down which tumbles a spectacular waterfall. These cliffs are mantled with tussock grass, *Spartina arundinacea*, on all but the steepest slopes. February 1968. Photograph: Nigel Wace.

Most of the island is covered with a thick entanglement of tussock grass and is occupied by many penguin rookeries.

Stoltenhoff Island

Stoltenhoff Island (Fig. 9) was named after the brothers Stoltenhoff, crew members of a whaling ship, who had asked to be landed on Inaccessible Island thinking they would make their fortune there in fur sealing. After nearly two years of disappointment and spartan existence they were taken off by HMS *Challenger* when she called in October 1873. Stoltenhoff Island lies about 1.6 km north-west of Middle Island and is approximately 460 m long by 135 m wide. Its vertical cliffs, varying from 70 m to 80 m high, rise sheer from the sea. Only at one site, below the cliffs on the north-west side, is it possible to land, but even there this is hazardous because of the ocean swell. Like Middle Island, the centre is flat topped, rising to 100 m high, and is densely overgrown with tussock grass.

Gough Island

Gough Island (Fig. 10) is so called because it was sighted in 1731 by Captain Gough, master of the barque *Richmond* bound for China. It was no doubt, however, the same island as that reported by the Portuguese in the 16th century and named by them as Gonçalo Alvarez after the captain of Vasco da Gama's flagship (Holdgate, 1958: 75). Sealers lived ashore for varying periods of up to two years during the 19th century (Wace, 1961: 337). There has been a manned weather station on the island since 1955.

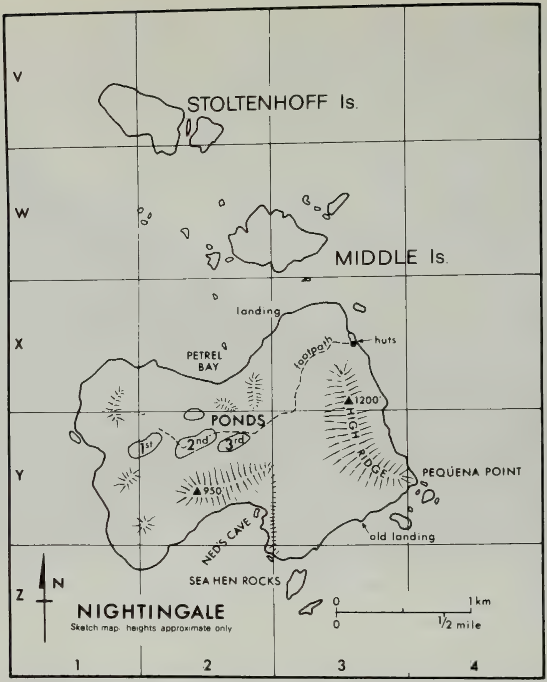
V
W
X
Y
Z
STOLTENHOFF Is.
MIDDLE Is.
landing
huts
PETREL BAY
footpath
1200'
HIGH RIDGE
PONDS
1st
2nd
3rd
PEQÚENA POINT
950'
NED'S CAVE
old landing
SEA HEN ROCKS
N
NIGHTINGALE
Sketch map· heights approximate only
0
1 km
0
½ mile
1
2
3
4

Fig. 9 Map of Nightingale Island with the subsidiary Stoltenhoff and Middle Islands to the north.

The island lies about 320 km south-south-east of Tristan da Cunha and is approximately 13 km long and 5–6 km wide. Steep cliffs skirt most of its coastline (Fig. 11), those at the north-east end being up to 370 m high. Rainfall, as previously mentioned, is high, and the waters of several falls drain down to the cliff edges and cascade precipitously into the sea. Landing is usually effected at the boulder beach at the entrance to a ravine known as the Glen (Fig. 12). The interior of the island is an undulating boggy plateau with an elevation of 610 m from which several peaks rise, the highest being Edinburgh, 910 m. Vegetation covers all the island except for the sheerest cliffs and the tops of the peaks, and has been adequately described by Wace (1961). The island is the only locality for the flightless Gough moorhen called 'Island cock' *Gallinula nesiotis comeri*, a different subspecies to that formerly occurring on Tristan da Cunha.

Visitors who have made vascular plant collections

Chronological list

The following list is a chronological list of persons, expeditions and ships known to have made vascular plant collections on the islands:

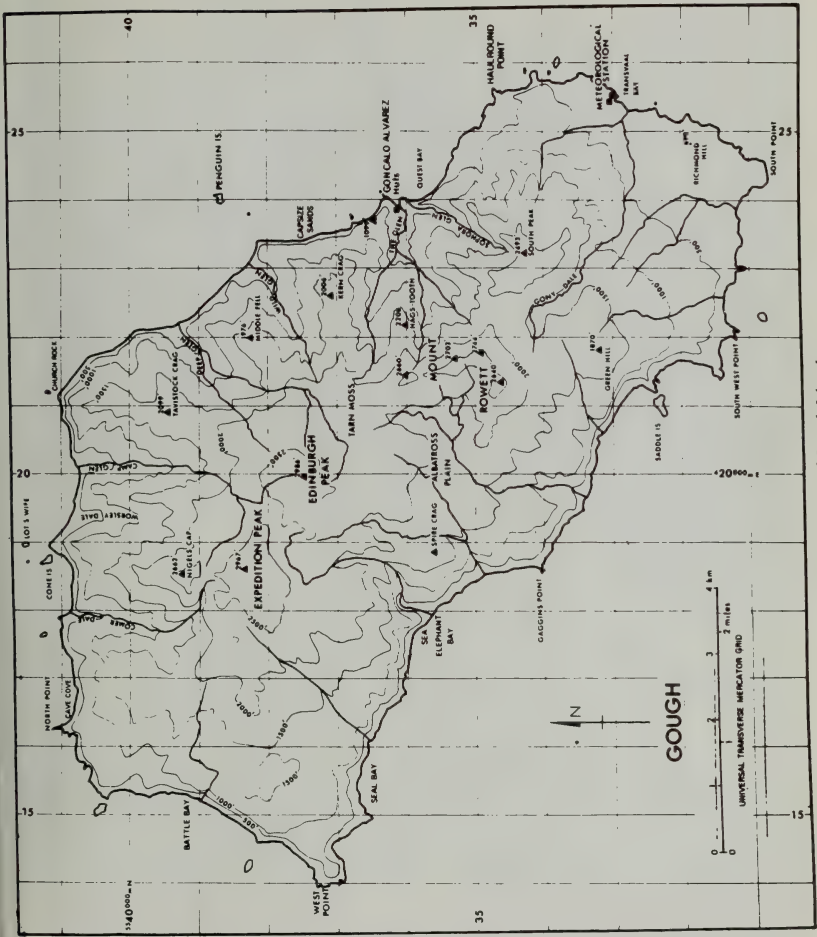
GOUGH
N
PENGUIN IS.
GONCALO ALVAREZ
HUTS
QUEST BAY
HAULROUND POINT
METEOROLOGICAL STATION
TRANSVAAL BAY
RICHMOND HILL
SOUTH POINT
SOUTH PEAK
SOPHORA GLEN
THE GLEN
CAPSIZE SANDS
KERN CRAG
HAGS TOOTH
MIDDLE FELL
GONY DALE
GREEN HILL
SOUTH WEST POINT
SADDLE IS
MOUNT ROWETT
TARN MOSS
ALBATROSS PLAIN
SPIRE CRAG
EDINBURGH PEAK
EXPEDITION PEAK
NIGELS CAP
TAVISTOCK CRAG
DEEP GLEN
CHURCH ROCK
CAMP GLEN
WORSLEY DALE
LOT'S WIFE
CONE IS
COWER DALE
NORTH POINT
CAVE COVE
BATTLE BAY
WEST POINT
SEAL BAY
SEA ELEPHANT BAY
GAGGINS POINT
UNIVERSAL TRANSVERSE MERCATOR GRID
2 miles
4 km
20000m E
5540000m N

Fig. 10 Map of Gough Island.

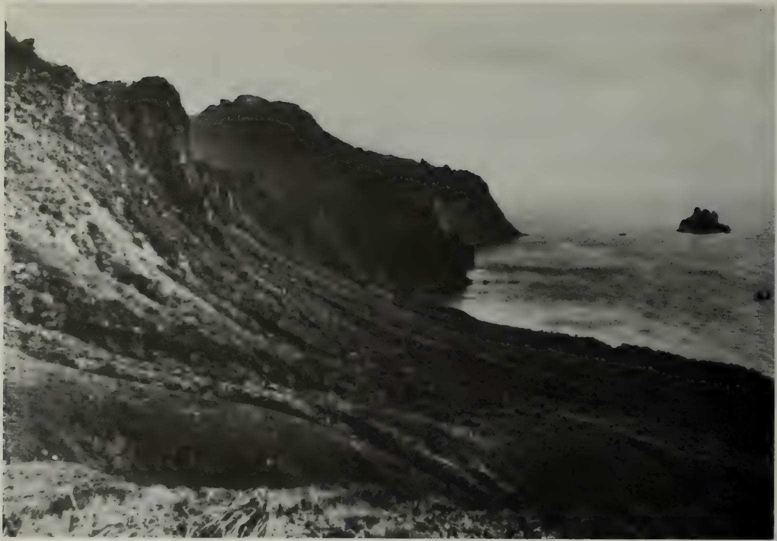

Fig. 11 East coast of Gough Island looking north towards Reef Point, with Penguin Islet (115 m) lying 0.8 km off the point. The lower slopes of Pummel Crag in mid-foregrounnd are covered with the tree fern *Blechnum palmiforme* and thickets of *Phylica arborea*. May 1968. Photograph: Nigel Wace.

Tristan da Cunha

3–7 January 1973	Aubert Du Petit-Thouars
1816–1817	Carmichael
12 November 1852	Macgillivray & Milne (HMS *Herald*)
15 October 1873	Moseley (HMS *Challenger*)
October 1873	Crosbie
October 1874	Saunders
July 1892	Richardson
February 1904	Bonomi
1908–1909	Keytel
20 May 1922	Wilkins (Shackleton-Rowett Expeditions in the SY *Quest* but see remarks on pp. 353 and 406 under *Polystichum mohrioides*.)
1922–1925	Rev. and Mrs Rogers
1926	Glass
10 November 1934	Siggeson
February–March 1937	Dyer (HMS *Carlisle*)
1937–1938	Christophersen & Mejland (Norwegian Scientific Expedition)
February 1939	MacCraken
1954–1956	Stableford
11–29 October 1955	Wace (Gough Island Scientific Survey)
February & March 1962	Dickson (Royal Society Expedition)
March 1968	Wace
1971–1974	Fleming
November and December 1976	Wace

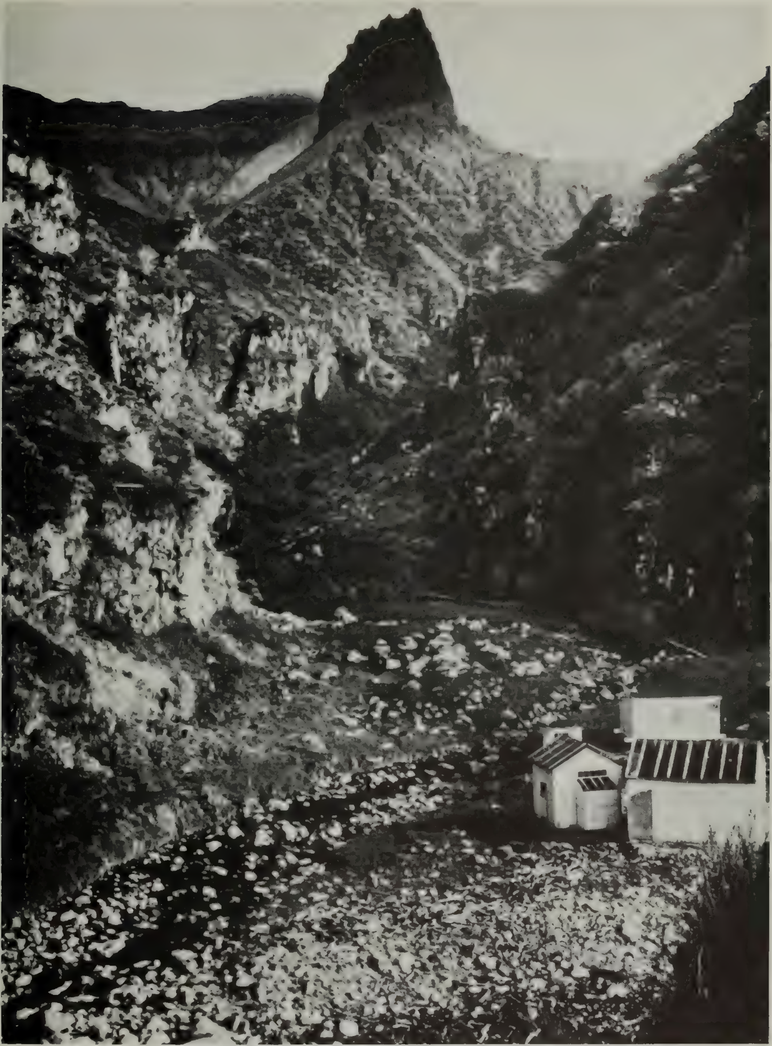

Fig. 12 Gough Island, looking up the Glen from Archway Rock to Hag's Tooth and Mt Rowett. The steep slopes are covered with the ferns *Blechnum palmiforme* and *Histiopteris incisa* var. *carmichaelina*, and with thickets of *Phylica arborea*. May 1968. Photograph: Nigel Wace.

	Inaccessible Island
16 October 1873	Moseley (HMS *Challenger*)
23 May 1922	Wilkins (Shackleton-Rowett Expedition in the SY *Quest*)
February 1938	Christophersen (Norwegian Scientific Expedition)
February 1957	Stableford
March 1962	Dickson (Royal Society's Expedition)
March 1968	Wace
September 1973–January 1974	Fleming
November 1976	Wace
	Nightingale Island
17 October 1873	Moseley (HMS *Challenger*)
1922–1925	Rev. & Mrs Rogers
February 1938	Christophersen (Norwegian Scientific Expedition)
1953–1954	Stableford (but see comments under alphabetical list of expeditions and visitors below regarding certain specimens labelled from Nightingale.)
March 1968	Wace
February 1972	Fleming
November 1976	Wace
	Middle Island
1 February 1938	Christophersen (Norwegian Scientific Expedition)
	Stoltenhoff Island
8 February	Christophersen (Norwegian Scientific Expedition)
	Gough Island
22 April 1904	Brown (Scottish National Antarctic Expedition in the SY *Scotia*)
1 June 1922	Wilkins (Shackleton-Rowett Expedition in the SY *Quest*)
8 June 1927	*'Discovery'* ('W.S.') Expedition
27 February 1933	Christensen
March 1955	Swain
28 November 1955–5 March 1956	Wace (Gough Island Scientific Survey)
March 1956	MacMillan
1956–1957	van der Merwe
February 1961	McKinnon
May 1968	Wace
January 1972	Fleming
November 1976	Wace

Alphabetical list

The following is an alphabetical list of personnel, expeditions and ships known to have made vascular plant collections on the islands, together with a note of the institutes where their collections are now deposited. Herbaria are denoted by their official abbreviations (see Holmgren & Keuken, 1974). The following collections were consulted during the preparation of this paper:

AAS = British Antarctic Survey (Botanical Section) Cambridge, England.
BM = British Museum (Natural History), London, England.
CGE = Botany School, The University, Cambridge, England.
E = The Royal Botanic Garden, Edinburgh, Scotland.
K = The Royal Botanic Gardens, Kew, Surrey, England.
NBG = Compton Herbarium, National Botanic Gardens, Kirstenbosch, Cape Town, South Africa.
O = Botanisk Museum, Oslo, Norway.
P = Laboratoire de Phanérogamie, Museum National d'Histoire Naturelle, Paris, France.
PRE = National Herbarium, Botanical Research Institute, Pretoria, South Africa.

AUBERT DU PETIT-THOUARS, AUBERT

A. Aubert Du Petit-Thouars (Fig. 13) was a traveller and botanist who visited Tristan da Cunha in 1793 when the vessel in which he was travelling to the Mascarenes made a five-day stay for watering. He was ashore on the island on the 3, 5 and 6 January, during which time he made the first known botanical investigation of the island and collected 100 species, including 25 flowering plants and 16 ferns (the remainder being non-vascular cryptogams). The first set of his material is at P with a few duplicates at BM. For the correct form of his name see Barnhart (1965: **1**:88); in the citation of specimens it has been abbreviated to Thouars. *Literature:* Aubert Du Petit-Thouars (1808).

BARKLY, HENRY

Two ferns, *Dryopteris aquilina* and *Elaphoglossum succisaefolium,* gathered whilst HMS *Challenger* visited Tristan da Cunha in 1873, are associated with Sir H. Barkly although probably not collected by him. The specimens are in BM.

BONOMI, P.

Nothing is known of P. Bonomi beyond the fact that he visited Tristan da Cunha and made a collection of flowering plants and ferns there in February 1904. The first set of these specimens is in NBG (transferred from the old South African Museum), with a few duplicates at K. On some sheets in NBG his name appears as P. Benomi—perhaps an alternative spelling.

BROWN, ROBERT NEAL RUDMOSE

R. N. R. Brown was botanist on the Scottish National Antarctic Expedition to the Weddell Sea, 1902–04. On his return, the expedition's ship SY *Scotia,* anchored for three days off Gough. Only on one day (22 April 1904) could a boat be got ashore because of continual high seas. Even then, because of the poor anchorage, the shore party had to keep within reach should sudden recall be necessary. Thus no visit to higher ground was possible. The first set of plants is at K, the second at E, and a few duplicates at BM. *Literature:* Brown (1905), Brown, Wright & Darbishire (1912).

HMS *CARLISLE*

See under Dyer.

CARMICHAEL, DUGALD

Captain Dugald Carmichael of the 72nd Regiment landed on Tristan da Cunha on 28 November 1816 with a British garrison sent to take possession of the island to prevent a possible attempt by the French to rescue Napoleon Bonaparte, imprisoned by the British on St Helena. Carmichael had been attached to the garrison at his own request in order to make a botanical survey of the island (Brander, 1940: 72). During the three months he was there he made a collection of vascular plants totalling 55 species (Hemsley, 1885: 138), some of which are at K and others at BM. *Literature:* Carmichael (1819), Hemsley (1885).

HMS *CHALLENGER*

See under Moseley.

CHRISTENSEN, LARS

Consul Lars Christensen, sponsor of several Norwegian Antarctic expeditions during the 1920-1939 period, landed on Gough on 27 February 1933 from MS *Thorshavn* when the ship was returning from the Antarctic at the end of the 1932–33 season. The plants gathered during the brief visit ashore were sent to Dr Erling Christophersen in Oslo. He found that among the 22 species collected by Christensen, 12 were new to the island of which three were new to science. The first set is at O. *Literature:* Christophersen (1934).

CHRISTOPHERSEN, ERLING and MEJLAND, YNGVAR

The bulk of the vascular plants collected during the Norwegian Scientific Expedition to Tristan da Cunha, 1937–38, were gathered by Erling Christophersen (leader and botanist)

(Fig. 16) although some were collected by Yngvar Mejland, botanical assistant and the expedition's handyman. Most of the collecting was done on Tristan itself, where the primary work of the expedition was carried out, but time was also spent on Nightingale and Inaccessible Islands during February 1938. No visit was possible to Gough Island, but a brief landing was made on both Middle and Stoltenhoff Islands and the few plants collected represent the first botanical specimens to be gathered from these subsidiary islands of Nightingale. The expedition departed from Tristan da Cunha on 29 March 1938. The first set of the vascular plants is at o, the second set at BM, the third at C and the fourth at K. Other smaller part sets are at P, PRE, BOL, GH and WELT. Although some duplicate sets of vascular plants of this expedition have both collectors' names appearing on the accompanying labels (either printed or hand written), the original set (O), as well as most of the other distributed sets, bears simply the name of either Christophersen or Mejland on each label followed by the relevant number allocated to that collector in the field. Material from this expedition cited throughout this present paper follows that sequence, thus:

Christophersen	1 – 100	1051 – 1109
	201 – 300	1111 – 1133
	351 – 600	1181 –1286
	628 – 631	1312 – 1335
	642	1577
	644 – 810	1652b
	825	2000 – 2236
	896	(Nightingale Is.)
	945	2300 – 3000
	955	(Inaccessible Is.)
Mejland	101 – 200	1041 – 1050
	301 – 350	1110
	601 – 627	1134 – 1179
	632 – 641	1287 – 1309
	643	1356 – 1576
	811 – 824	1591 – 1650
	1011 – 1014	1654 – 1738
	1017 – 1038	1745 – 1820

Literature: Narrative: Christopherson (1940), Crawford (1941); Botanical: Christensen, C. (1940), Christophersen (1934, 1937, 1940*b*, 1944, 1968), Hooper (1968).

Crosbie, A.

Dr A. Crosbie was staff surgeon in the Royal Navy on board HMS *Challenger* during that vessel's oceanographic expedition of 1872–1876. He collected a few ferns (including *Blechnum australe* and *Huperzia insularis*) on Tristan da Cunha when a landing was made there in October 1873. These subsequently became the property of William Evans and were presented by his son to the herbarium at E in 1933.

Dickson, James Holms

J. H. Dickson was botanist with the Royal Society's expedition to Tristan da Cunha in 1962, to assess the damage caused to both the flora and fauna by the eruption of the island's volcano in 1961. Vascular plants, together with bryophytes and lichens, were collected between 2 February and 17 March 1962 mostly on Tristan da Cunha, but a visit was also made to Nightingale (1 & 2 March) and Inaccessible (4 March). The first set of vascular plants is at BM with a few duplicates at K, AAS and CGE. *Literature:* Dickson (1965*a*), Dickson (1965*b*), Wace and Dickson (1965).

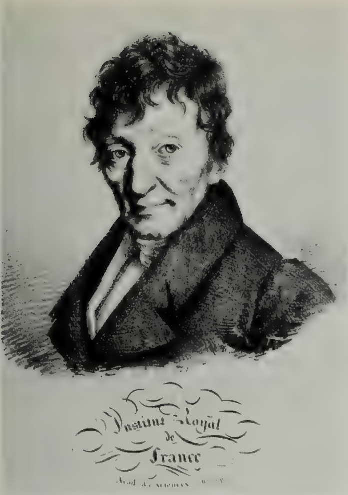
Institut Royal
de
France

Fig. 13 Aubert Aubert Du Petit-Thouars.

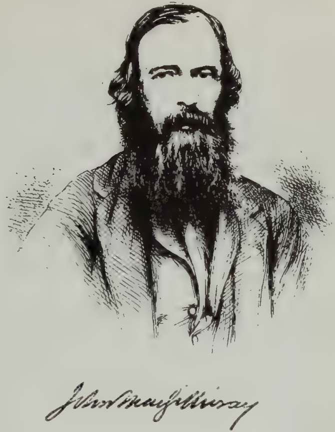
John Macgillivray

Fig. 14 John Macgillivray.

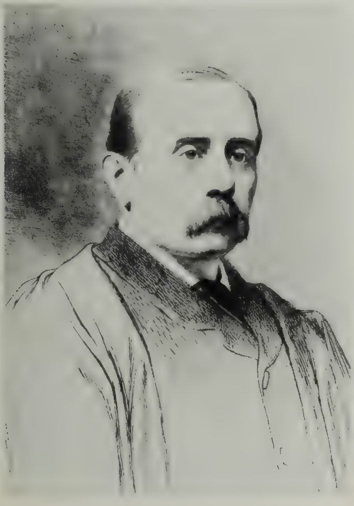

Fig. 15 Henry Nottidge Moseley.

Fig. 16 Erling Christophersen.

DISCOVERY INVESTIGATIONS
During the return from the 1926–27 *Discovery* investigations, the RRS *William Scoresby*, which had been on whale-marking and oceanographical surveys with RRS *Discovery II* off South Georgia and the Falklands, called in at Gough Island on 8 June 1927. Sir Alister Hardy (1967: 433–437) marine zoologist, writing of this cruise, describes the landing and subsequent climb up to about 370 m along a central ridge leading up to Mt Howett. His two companions, who collected both zoological and botanical material, are identified (Hardy, 1967: 434) as Dilwyn John (zoologist) and Rolfe Gunther (zoologist). The latter, in his account of the whole expedition (Gunther, 1928: 41), also mentions this short visit to Gough Island. The plant material (allocated Station No. 123) was brought back in formalin, as was usual with zoological specimens, and was presented to the BM, where it was subsequently dried and placed in the herbarium. *Literature:* Hardy (1967), Gunther (1928).

DU PETIT-THOUARS
See under Aubert Du Petit-Thouars.

DYER, ROBERT ALLEN
R. A. Dyer (Fig. 17) was seconded from the South African Government's Division of Botany to join the HMS *Carlisle* expedition to Tristan da Cunha in 1937. The ship had been sent by the British Admiralty to take provisions and mail to the island, to investigate the general conditions and health of the inhabitants, and to embark the resident minister, the Rev. H. Wilde, for leave. It arrived from Cape Town on 28 February 1937 and stayed three days. Plant collections were made ashore by Dyer on two days; on the 1 March near the beach landing stage and margin of the Settlement Plateau and on the 2 March (with the help of an islander, Arthur Rogers) up the slopes of the Peak to 760 m. Dyer (1939) records the species he collected, and gives a list of some pasture grasses and species of trees and shrubs brought from South Africa that were intended to be established on the island. The first set of Dyer's Tristan plants is at PRE, the second at NBG; smaller part sets are at BM, K and O. *Literature:* Dyer (1939).

FLEMING, J. I. H.
J. I. H. Fleming served as Government Administrator on Tristan da Cunha from 1971 to 1974 and made a collection of about 100 numbers of flowering plants and ferns, not only from Tristan da Cunha, but also from Gough Island (January 1972), Nightingale Island (February 1972) and Inaccessible Island (September 1973 to January 1974). His specimens are at E.

GLASS, DONALD
D. Glass was a Tristan islander who collected a few flowering plants and ferns on Tristan da Cunha in 1926. These were subsequently forwarded to Mrs Meade-Waldo of Edenbridge, Kent, who presented them to the BM in 1927.

GOUGH ISLAND SCIENTIFIC SURVEY, 1955–56
See under Wace.

HMS *HERALD*
See under Macgillivray and Milne.

KEYTEL, P. C.
P. C. Keytel visited Tristan da Cunha on two occasions: first in 1907, then for a more prolonged stay in March 1908 to negotiate a trade in sheep and dried fish between the islanders and the South African market (Munch, 1971: 70–80). His second visit lasted a year (1908–09), during which time he made a botanical collection of 57 species (43 flowering plants and 27 ferns) (Phillips, 1913). The first set of his material is at NBG (transferred, like those of P. Bonomi (q.v.), from the old South African Museum); and a few duplicates are at K. *Literature:* Phillips (1913).

McCRAKEN, M. L.
Nothing is known of McCraken except that he gathered a specimen of *Chenopodium tomentosum* on Tristan da Cunha in February 1939 which is now at BM.

MACGILLIVRAY, JOHN and MILNE, WILLIAM GRANT
The two collectors John Macgillivray (Fig. 14) and William G. Milne were naturalist and assistant naturalist respectively on board HMS *Herald* (under the command of Captain H. M. Denham) during that ship's second surveying voyage in 1852–61 to the Pacific and Indo-Pacific waters. On the outward voyage the ship called at Tristan da Cunha in November 1852 and it seems that both naturalists collected at the same localities while ashore. According to Hemsley (1885: 139) about 40 species of vascular plants, together with a few mosses and hepatics, were collected. Macgillivray's specimens are mainly at BM and a few are at K; Milne's specimens are at K with possibly some at CGE. Those at BM and K include both a numbered and an unnumbered series. It should be noted that Macgillivray (and his father) wrote his name in this way, and not as 'MacGillivray' (Barnhart, 1965: **2**:424). *Literature:* Botanical specimens are cited throughout Hemsley (1885).

McKINNON, R. S.
R. S. McKinnon, whilst serving as a naval officer on the Royal Naval Survey vessel HMS *Owen,* collected a few numbers of ferns on Gough Island in February 1961. These are now at K.

MACMILLAN, R. A. B.
MacMillan visited Gough Island in May 1956 and gathered a few numbers of flowering plants and ferns which are now at PRE.

MEJLAND, YNGVAR
See under Christophersen and Mejland.

MERWE, J. J. VAN DER
J. J. van der Merwe was meteorologist to the Gough Island Scientific Survey expedition 1955–56. He then remained on that island for a further two years in charge of the meteorological station, set up by the South African Weather Bureau, after the expedition had left. During 1956–58 van der Merwe made a small collection of plants, the first set of which is at PRE, with a few duplicates at K and BM. *Literature:* A few specimens are cited in Wace & Dickson (1965: Appendix A).

MILNE, WILLIAM GRANT
See under Macgillivray and Milne.

MOSELEY, HENRY NOTTIDGE
H. N. Moseley (Fig. 15) was appointed naturalist to HMS *Challenger* during its world oceanographic voyage of 1872–76. On the outward voyage the ship called at the Tristan group of islands. It arrived at Tristan da Cunha on 15 October 1873 and immediately Moseley was able to embark he began botanizing. He was ashore for six hours before being recalled to the ship because of a heavy squall. The ship visited Inaccessible Island the next day (16 October) and Nightingale Island on 17 October, before sailing for Cape Town on 18 October 1873. Hemsley (1885: 139) states that Moseley collected in all 45 species of vascular plants from the three islands he visited (38 species on Tristan da Cunha, 21 species on Inaccessible Island, and 10 species on Nightingale Island). Of the vascular plants, the first set seems to be at K and the second at BM, with a few duplicates at E. A few Moseley specimens from these islands are also at CGE (see Gilmour and Tutin, 1933: 24). *Literature:* Narratives: Spry (1877), Moseley (1879 and subsequent editions), Linklater (1972); botanical: Moseley (1874), Hemsley (1885).

NORWEGIAN SCIENTIFIC EXPEDITION TO TRISTAN DA CUNHA, 1937–38
See under Christophersen and Mejland.

RICHARDSON, J.
Nothing is known of Richardson except that he gathered the fern *Lycopodium diaphanum* on Tristan da Cunha in July 1892. The specimen is now in O.

ROGERS, HENRY M. and ROGERS, ROSE A.
Rev. H. M. Rogers was missionary-priest on Tristan da Cunha from 1 April 1922 until 4 February 1925. While there he made, together with his wife, a small collection of plants consisting of 20 numbers (12 flowering plants, 7 ferns and 1 moss), which were presented to BM, with a few duplicates to K. The identification of this collection appeared as part (pp. 212–213) of Appendix II to the book later written by Mrs Rogers on their experiences during three years stay on the island. The Rev. Rogers died on 14 May 1926. *Literature:* Rogers (1926).

ROYAL SOCIETY EXPEDITION TO TRISTAN DA CUNHA, 1962
See under Dickson.

SAUNDERS, W. W.
Nothing is known of W. W. Saunders except that he gathered a specimen of *Rumex angiocarpus* on Tristan da Cunha in October 1874 which is now at K.

SCOTTISH NATIONAL ANTARCTIC EXPEDITION, 1902–04
See under Brown.

SHACKLETON-ROWETT ANTARCTIC EXPEDITION, 1921–22
See under Wilkins.

SIGGESON, EINAR
On the voyage to the southern Antarctic whaling grounds during the 1934–35 season, the Norwegian whaler *Thorshammer* made a stop at Tristan da Cunha on 10 November 1934 to put ashore Mr Einar Siggeson, a whaling captain, who, at the the request of Consul Lars Christensen, had been asked to collect plants and animals. The plants thus gathered were forwarded to the Botanical Museum at Oslo in the spring of the following year. When examined by Dr Erling Christophersen, the collection was found to include 36 species including 17 flowering plants and 5 ferns, one of which was new to the Tristan flora. *Literature:* Christophersen (1937: 8–13).

STABLEFORD, H. GERALD
H. G. Stableford served as agricultural officer on Tristan da Cunha from 1953–57 (Munch, 1971: 246). While there he visited other islands in the group and on his return to England brought back flowering plants and ferns that he had gathered on Tristan da Cunha (1954–56), Inaccessible Island (February 1957) and Nightingale Island (1954). A few, although not all, of the herbarium specimens at K labelled to have come from Nightingale were undoubtedly collected on Tristan. Two sets of plants were gathered, although the material in each does not seem to be mutually exclusive. One set was deposited at BM, and the other at K. The BM set was found to have several duplicated series of numberings, and so after receipt the whole collection was in consequence renumbered as a single consecutive series in order to avoid future confusion. The BM now has numbers running from 1-132. The set of plants at K consists of a numbered series (several numbers being repeated) as well as unnumbered series, presumably in much the same condition as it was received. The present situation is unfortunate because material of the same gathering in both herbaria often does not bear the same number. *Literature:* Some specimens are cited in Wace & Dickson (1965: Appendix A).

SWAIN, ADAM
An islander who in March 1955 collected a few ferns on Gough Island, now in the herbarium at K.

THOUARS
see under Aubert Du Petit-Thouars.

Fig. 17 Robert Allen Dyer.

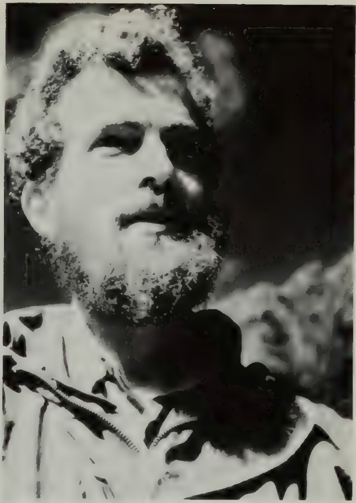

Fig. 18 Nigel M. Wace.

WACE, NIGEL M.

N. M. Wace (Fig. 18) was botanist to the Gough Island Scientific Survey of 1955–56. The expedition first landed on Tristan da Cunha, where they stayed from 1 October to 13 November 1955 and from whence they sailed in the *Tristania* (a 600-ton fishing vessel belonging to the Tristan da Cunha Development Company) to Gough Island. The expedition remained on Gough Island for six months from 14 November 1955 until they were taken off the South African naval frigate *Transvaal* on 13 May 1956, and returned then to Tristan da Cunha briefly before sailing for Cape Town. An account of the work of the entire expedition has been published by Holdgate (1958). Regarding the vascular plants collected during the expedition, two series were gathered: 94 numbers from Tristan da Cunha (each prefixed with the letter T) and 163 numbers from Gough Island (without prefix). The first set of all numbers is at BM. Wace visited the Tristan group again from March to May 1968 during which period he was able to make further collections on Tristan da Cunha (including many species colonizing the volcanic debris resulting from the eruption of 1961), and on Inaccessble, Nightingale and Gough Islands. A further expedition to these four major islands was made by him from November to December 1976. At the time of writing (1979) duplicates of only the grasses, sedges and rushes have so far been distributed from the 1968 and 1976 expedition, specimens of which have been lodged at Kew. *Literature:* Narrative: Holdgate (1958); Botanical: Wace & Holdgate (1958), Wace (1961).

WILKINS, GEORGE HUBERT

G. H. Wilkins was appointed naturalist to the Shackleton-Rowett Antarctic Expedition of 1921–22. On returning from the Antarctic, the expedition's vessel, the SY *Quest,* visited several islands of the Tristan-Gough group: Tristan da Cunha (20 May 1922), Nightingale Island (21 May), Inaccessible Island (23 May) and Gough Island (28 May to 2 June), before sailing for Cape Town on 3 June 1922. No vascular plants were collected on Tristan da Cunha (except perhaps for the fern *Polystichum mohrioides,* see p. 406) or on Nightingale

Island, but a small collection was made on Inaccessible Island as well as on Gough Island. Wilkins was able to go ashore on the latter for five out of the six days they were there, although landing was difficult in deteriorating weather conditions (Wild, 1923: 265–286). Wilkins (1925: 68–70) lists those species (including 13 flowering plants and 9 ferns) he collected on Gough Island, but not all of these have since been traced at BM, to which the whole of the Shackleton-Rowett expedition's plant collections were presented. *Literature:* Narrative: Wild (1923); Botanical: Wilkins (1925).

RRS *William Scoresby*
See under *Discovery* Investigations.

Systematic list

SPERMATOPHYTA

The families are arranged by a modified Bentham & Hooker system. The species appear alphabetically within each family.

RANUNCULACEAE

[**Ranunculus acris** L.
This species is given as occurring on Tristan da Cunha in Wace & Dickson (1965; 334 and in Appendix A) and said to be based on an unpublished collection in BM. Unfortunately no material in that herbarium has been traced to substantiate this record.]

Ranunculus carolii Christoph.
Endemic. This species was described by Christophersen (1950: 186) from a specimen found by Mejland on Tristan during the Norwegian Scientific Expedition 1937–38. However, a specimen collected on that island by Carmichael in 1817, since identified as this species, is the earliest record for the group. It has also been found on Gough by Wace in 1955. The species is regarded by Christophersen (1968: 8) as being endemic and closely related to *R. biternatus* Sm. *(R. crassipes* J. D. Hook.)

Tristan: *Carmichael* s.n. (BM); *Christophersen* 60 (O), 550d (O) 1777 (O); *Mejland* 1369 (O-holotype, BM), 1558 (O); *Wace* T.71 (BM). **Nightingale:** *Stableford* s.n. (K) [Likely to be in error for Tristan]. **Gough:** *Wace* 26 (BM), 28 (BM), 51 (BM), 78 (BM), 144 (BM).

Ranunculus repens L.
Introduced. First noted from Tristan da Cunha in 1938 as a weed near a garden and also at the Potato Patches.

Tristan: *Christophersen* 1788 (O, BM); *Mejland* 1288 (O, BM).

CRUCIFERAE

Brassica juncea (L.) Czernj.
Introduced. Found on Tristan da Cunha in pasture at Anchorstock Bay in 1938.

Tristan: *Mejland* 1411 (O, BM).

Brassica rapa L.
Introduced. Found as weed in gardens at the Settlement on Tristan da Cunha in 1938 and around ruined cottage at Saltbeach, Inaccessible Island, in 1962.

Tristan: *Mejland* 340 (O, BM) [under *Brassica campestris* L. in *Christophersen*, 1968: 9]. **Inaccessible:** *Dickson* 127 (BM), 128 (BM).

Cardamine glacialis (G. Forster) DC.
C. propinqua Carmich.
Native. First discovered on Tristan da Cunha by Carmichael in 1817 and described by him as *C. propinqua* (Carmichael, 1819: 507). This was later found to be the same as *C. glacialis*

originally described by G. Forster as *Sisymbrium glaciale* in 1789 from material collected in Tierra del Fuego

Tristan: *Carmichael* s.n. (BM-holotype of *C. propinqua*); *Christophersen* 517 (O), 534 (O), 1275 (O); *Dickson* 109 (BM). **Inaccessible:** *Christophersen* 2348 (O); 2500 (O). **Gough:** *Lars Christensen* s.n. (O); *van der Merwe* 26 (K); *Wace* 25 (BM), 25a (BM), 145 (BM).

Coronopus didymus (L.) Sm.

Introduced. First recorded from Tristan da Cunha by Stableford near the Settlement in 1954.

Tristan: *Stableford* s.n. (K), 7 (BM); *Dickson* 19 (BM).

Nasturtium officinale R.Br.

Introduced. Discovered on Tristan da Cunha by Dickson in 1962 by the Big Watron Waterfall* near the Settlement.

Tristan: *Dickson* 144 (BM)†.

Raphanus sativus L.

Introduced. Aubert Du Petit-Thouars (1808: 46) reported this species from Tristan da Cunha, growing in a small area which was at one time under cultivation. Herbarium material from Inaccessible Island, which was collected at Saltbeach by Christophersen in 1937, is no doubt also a relic of former agrarian activities.

Tristan: *Thouars* s.n. (P). **Inaccessible:** *Christophersen* 2622 (O).

CARYOPHYLLACEAE

Cerastium fontanum subsp. **triviale** (Link) Jalas

C. triviale Link; *C. caespitosum* subsp. *triviale* (Link) Hiit.; *C. caespitosum* Gilib.; *C. holosteoides* Fr.

Introduced. Has been found in small quantity in grassland turf of the Settlement Plain on Tristan da Cunha, and also in several localities at Blenden Hall on Inaccessible Island. It was found on Gough Island for the first time in 1972.

Tristan: *Bonomi* 16 (NBG); s.n. [herb. Mus. Austro-Afric. 1145] (NBG); *Christophersen* 13 (O, BM), 44 (O, BM); *Dickson* 76 (BM) 94 (BM); *Dyer* 3532 (PRE, K); *Keytel* 1792 (NBG, K); *Macgillivray* 352 (K); *Mejland* 175 (O), 611 (O); *Moseley* s.n. (BM), s.n. (K); *Siggeson* 40 (O); *Stableford* 17 (BM), 105 (BM), s.n. (K); *Wace* T.72 (BM), T.79 (BM). **Inaccessible:** *Christophersen* 2303 (O, BM), 2381 (O); *Moseley* s.n. (BM, K, E). **Gough:** *Fleming* 2 (E).

Polycarpon tetraphyllum (L.) L.

Introduced. First recorded from Tristan da Cunha by Macgillivray during the visit of HMS *Herald* to the island in November 1852 and since found in pastures and on open ground.

Tristan: *Christophersen* 276 (O); *Dickson* 35 (BM); *Macgillivray* 351 (K); *Mejland* 120 (O, BM), 126b (O); *Moseley* s.n. (K, E); *Stableford* s.n. (K).

Scleranthus annuus L.

Introduced. Recorded on Tristan da Cunha by Stableford in 1954 in the grounds of the Settlement mission.

Tristan: *Stableford* 5 (BM).

Silene alba (Mill.) Krause

Introduced. Found on Tristan da Cunha during 1955–56, occurring as a weed at the Settlement.

Tristan: *Stableford* 119 (BM).

Silene gallica L.

Introduced. Discovered on Tristan da Cunha during the summer of 1954 in the Mission garden at the Settlement, where it occurred as a weed.

Tristan: *Stableford* 2 (BM).

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* Wace *(in litt.)* states that this is not called 'Big Watron Waterfall' now as the 1961 eruption altered the topography of the area.

† No specimen has been traced which substantiates Stableford's record of this species from Tristan da Cunha as listed in Wace & Dickson (1965, Appendix A).

Spergula arvensis L.
Introduced. Discovered on Tristan da Cunha during 1955–56 growing as a weed at the Settlement; probably introduced with imported seed.

Tristan: *Stableford* 110 (BM).

Stellaria media (L.) Vill.
Introduced. Originally collected on Tristan da Cunha by Christophersen in 1937 as a weed in the Potato Patches and then on Gough Island by Wace in 1955, growing between boulders and under *Rumex obtusifolius* above the beach.

Tristan: *Christophersen* 291 (O, BM), 295 (O, BM); *Mejland* 171 (O).* **Gough:** *van der Merwe* 59 (PRE); *Wace* 4 (BM).

MALVACEAE

Malva parviflora L.
Introduced. First recorded in pastures on Tristan da Cunha by Macgillivray in 1852. It has since been found in a meadow and a garden near the Settlement, presumably in the latter site as a weed.

Tristan: *Dickson* 45b (BM); *Macgillivray* s.n. (K); *Mejland* 101 (O, BM), 1293 (O); *Siggesson* 41 (O); *Stableford* 14 (BM).

[**Malva sylvestris** L.
This species is recorded from Tristan by Wace & Dickson (1965, Appendix A) who cite Christophersen (1937). Christophersen, however, merely quotes Hemsley's reference to this species (Hemsley, 1885: 145). The latter author listed introduced species known at that date from the Tristan group based on material in the collections of Aubert Du Petit-Thouars, Carmichael, Macgillivray, Milne and Moseley. The material of all these collectors is still extant but only one of them collected a *Malva*. This specimen, which was gathered by Macgillivray and is in the Kew herbarium, is not *Malva sylvestris* but *M. parviflora* (q.v.).]

GERANIACEAE

Geranium dissectum L.
Introduced. First recorded on Tristan da Cunha by the Norwegian Scientific Expedition of 1937–38 as a weed occurring outside the Settlement gardens and in pasture at the Potato Patches.

Tristan: *Christophersen* 162 (O, BM) 293 (O), 1290, (O, BM).

Pelargonium grossularioides (L.) Aiton
P. acugnaticum Thouars; *P. australe* var. *acugnaticum* (Thouars) Hemsley

Native. First recorded by Aubert Du Petit-Thouars on Tristan da Cunha in 1793 and described by him as *P. acugnaticum*. It was subsequently reduced to a variety of *P. australe* Willd. by Hemsley (1885: 147) and identified with *P. grossularioides* by Kunth (1912: 410). Christophersen (1968: 13), however, still considers, as did Aubert Du Petit-Thouars, that it is taxonomically distinct; until further critical work it is perhaps best to retain it under *P. grossularioides*.

Tristan: *Bonomi* 13 (NBG [herb. Mus. Austro-Afric. 1144], K,E); *Carmichael* s.n. (BM, K); *Christophersen* 244 (O), 277 (O, PRE); *Dickson* 15 (BM); *Dyer* 3547 (PRE, NBG, BM, K, O); *Glass* s.n. (BM); *Keytel* 1793 (NGB, K, BM), s.n. (PRE [herb. Marloth 4720]); *Mejland* 338 (O, BM); *Moseley* s.n. (K); *Rogers* 7 (BM), s.n. (K); *Stableford* 20 (BM), s.n. (K); *Thouars* s.n. (P-holotype of *P. acugnaticum*, BM). **Inaccessible:** *Christophersen* 2572 (O), 2547 (O, BM); *Moseley* s.n. (BM, K); *Stableford* 132 (BM).

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* No specimen has been traced to substantiate the Dickson record of the species from Tristan da Cunha as listed in Wace & Dickson (1965, Appendix A).

OXALIDACEAE

Oxalis corniculata L.

Introduced. Occasional near houses or as a garden weed on Tristan da Cunha, and on Inaccessible Island. Christophersen (1968: 13) states that this cosmopolitan species was first collected on Tristan da Cunha by Macgillivray in 1852, quoting Hemsley (1885: 147). Hemsley (loc. cit.) cites also a Moseley specimen from the Tristan da Cunha and one from Inaccessible Island. Voucher specimens for these records are at K and BM.

Tristan: *Christophersen* 124b (O, BM); *Dyer* 3535 (PRE); *Green* (for *Rogers*) 12 (BM); *Keytel* 1795 (NBG), s.n. (NBG [herb. Mus. Austro-Afric. 14609]); *Macgillivray* 350 (K); *Mejland* 106 (O); *Milne* s.n. (K); *Moseley* s.n. (K, BM); *Siggesson* 44 (O); *Stableford* 8 (K), 23 (BM). **Inaccessible:** *Christophersen* 2619 (O); *Dickson* 129 (BM); *Moseley* s.n. (K).

Oxalis purpurea L. TRISTAN SUNFLOWER

O. variabilis Jacq.

Introduced. First recorded from Tristan da Cunha by Keytel during 1908–09. This species occurs occasionally near houses at the Settlement and in the pasture near Waterun. Wace in 1955 notes that it was apparently spreading only vegetatively.

Tristan: *Keytel* 1794 (NGB, K, BM); *Stableford* 11 (BM), s.n. (K); *Wace* T.85 (BM).

RHAMNACEAE

Phylica arborea Thouars ISLAND TREE

P. nitida auct.

Native. First collected on Tristan da Cunha in January 1793 by Aubert Du Petit-Thouars, who based his type description on the material he gathered there (Aubert Du Petit-Thouars, 1811: 45). Along with the ferns *Histiopteris incisa* var. *carmichaeliana* and *Blechnum palmiforme*, this semi-procumbent evergreen tree forms dense communities at lower altitudes on most of the islands. Most of the larger growth near the coastal strips on Tristan da Cunha has, in the past, been cut down, as it provided (and still does) a readily available source of fuel (Fig. 19).

Tristan: *Bonomi* 20 (NBG [herb. Mus. Austro-Afric. 1143], K); *Carmichael* s.n. (BM), s.n. (K); *Christophersen* 426 (O, BM), 1133 (O, BM), 1816 (O); *Dickson* 11 (BM), 79 (BM); *Dyer* 3552 (PRE, NBG, BM, K, O); *Fleming* 43 (E), 44 (E); *Keytel* 1796 (NBG, K, BM), s.n. (PRE [ex Herb Marloth]); *Macgillivray* 357 (K); *Mejland* 613 (O), 1137 (O), 1412 (O, BM), 1816 (O); *Milne* 7 (K); *Moseley* s.n. (K, BM, E); *Rogers* s.n. (fasciated) (K); *Stableford* 55 (BM); *Thouars* s.n. (P-holotype); *Wace* T 20 (BM). **Inaccessible:** *Christophersen* 2309 (O, BM), 2441 (O), 2442 (O), 2547 (O, BM); *Moseley* s.n. (K, BM, E. CGE). **Nightingale:** *Christophersen* 2062 (O, BM), 2105 (O, BM); *Fleming* 58 (E); *Moseley* s.n. (BM, K); *Rogers* s.n. (K); *Stableford* 6 (K). **Stoltenhoff:** *Christophersen* 2143 (O), 2147 (O, BM). **Gough:** *Brown* s.n. (K, E); *Christensen* s.n. (O); *Discovery 'W.S' Exped.* s.n. (BM); *MacMillan* 1 (PRE); *van der Merwe* 37 (PRE), 50 (PRE, K); *Wace* 63 (BM), 103 (BM), *Wilkins* 38 (BM).

LEGUMINOSAE

Medicago polymorpha L.

M. denticulata Willd.

Introduced. Found growing on manure in the bull pen near the Mission gardens on Tristan during the summer of 1954. Stableford, who discovered it, considers it was probably introduced with imported dried fodder from South Africa.

Tristan: *Stableford* 4 (BM, K), 4a (K).

Medicago sativa L.

Introduced. Collected on Tristan by Stableford in the summer of 1954 at Sandy Point, and believed by him to have been introduced to the island in 1953 with imported fodder.

Tristan: *Stableford* 6 (K), 39 (BM), s.n. (K).

Sophora microphylla Ait.

Edwardsia macnabiana Graham; *Sophora tetraptera* var. *microphylla* J. D. Hook.; *Sophora tetraptera* forma *goughensis* E. G. Baker & Wilk.; *S. macnabiana* auct.

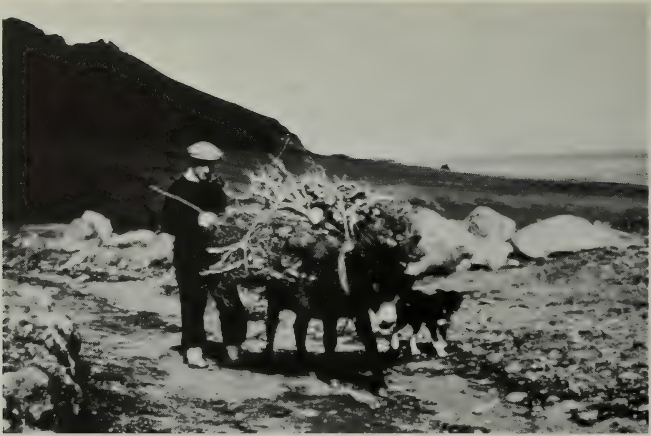

Fig. 19 Gilbert Lavarello transporting on a donkey wood of the island tree, *Phylica arborea*, used for fuel. Tristan da Cunha. October 1966. Photograph: George Edwards.

Native. Recorded only on Gough Island. Brown, Wright & Darbishire (1912: 33) mention that a sealer, George Comer, kept a diary during his six-month stay on the island with his companions from August 1888 to January 1889. In it he noted 'two kinds of trees' he found growing in the interior (Verrill, 1895). Brown, Wright & Darbishire (loc. cit.) point out that one of these trees was undoubtedly *Phylica nitida (= arborea),* which would have certainly been familiar to Comer and the other sealers, and also to the islanders of Tristan da Cunha, from its presence on the latter island as a main source of fuel. The identity of the second tree is most likely to have been *Sophora microphylla.* Herbarium material of this *Sophora* from Gough Island was first collected by Wilkins (naturalist on the Shackleton-Rowett Antarctic Expedition) in June 1922, and his material became the type of the form *goughensis* which he described with Baker (Wilkins, 1925: 68). Sykes & Godley, after a study of the long-distance ocean dispersal of the southern hemisphere *Sophora* species, along with a comparison of plants raised from seed in their experimental garden at Christchurch, New Zealand, concluded that the Gough Island species was not *S. tetraptera, S. prostrata* or *S. macnabiana* (as has been designated at various times) but only a race of *S. microphylla.* Furthermore the Gough Island plants (along with those from southern Chile and Chatham Islands), although lacking the juvenile form of some New Zealand races of *S. microphylla,* 'differ no more than the New Zealand races do one from another' and all have the same chromosome number 2n = 18 (Sykes & Godley, 1968: 495). Markham & Godley (1972: 639) consider that source of seed for the Gough Island population originated from Chile.

Gough: *van der Merwe* 27a (BM) 38 (K); *Wace* 27 (M); *Wilkins* 92 (BM -syntype of forma *goughensis*), 93 (BM -syntype of forma *goughensis*).

Trifolium dubium Sibth.
Introduced. First recorded on Tristan da Cunha in 1937 in pasture meadow, at the Settlement and at the Potato Patches. The plant has been found several times on the island since that date.

Tristan: *Christophersen* 273 (O, BM), 286 (O, BM): *Dickson* s.n. (BM); *Mejland* 136b (O), 163 (O, BM); *Stableford* 10 (K), 22 (BM), 104 (BM).

Trifolium micranthum Viv.

Introduced. Recorded on Tristan da Cunha by Wace in 1955 as abundant in close-grazed pastures around the Settlement.

Tristan: *Wace* T.92 (BM).

Trifolium pratense L.

Introduced. First noted on Tristan by Dyer in 1937 growing in pasture (Dyer, 1939: 604) although the first substantiative herbarium specimen was not collected until 1953–54 by Stableford, who considered that its presence on the island was due to imported seed.

Tristan: *Stableford* 3 (K).

Trifolium repens L.

Introduced. The earliest collection was made by Bonomi on Tristan da Cunha in 1904.

Tristan: *Bonomi* s.n. (NBG [herb. Mus. Austro-Afric. 1142]; *Christophersen* 275 (O), 1453 (O); *Keytel* 1812 (NGB, K, BM); *Mejland* 166 (O, BM); *Stableford* 5 (K).

Trifolium subterraneum L.

Introduced. This plant is noted in a recent paper by Wace & Holdgate (1976: 45) as being a species introduced with others 'as an impurity amongst grass seed for the playing field' at the Settlement on Tristan da Cunha. It seems that in 1968 it was confined to that locality, although as those authors have pointed out 'it may in future play an important part in the islander's economy by increasing the productivity of the pastures' (Wace & Holdgate, loc. cit.).

Ulex europeaeus L.

Introduced. Originally noted from Tristan da Cunha by Mrs F. M. Barrow, who states that there were 'a few bushes only near the houses' (Barrow, 1910: 277). The only herbarium specimen appears to be that of Mejland, 1937.

Tristan: *Mejland* 141 (O, BM).

ROSACEAE

Acaena sarmentosa (Thouars) Carmich. DOG CATCHER

A sanguisorbae auct., non Vahl: *Ancistrum sarmentosum* Thouars.

Native. This procumbent subshrub had been recorded from the four major islands, where it usually occurs amongst grass in open areas. Bitter (1911: 277–278) distinguished three varieties, the differences being mainly based on size and shape of the leaves and leaflets: a large-leaved variety, var *longiuscula* Bitter from Inaccessible Island; a small-leaved variety, var. *lusciniae* Bitter from Nightingale Island; and an intermediate variety, var *tristanensis* Bitter* from Tristan da Cunha, having leaves midway in size between the other two. These differences are not, however, accepted by Christophersen (1968: 10), as the material he collected on Nightingale and Inaccessible Islands, as well as that of other collectors cited below (most of which he examined), does not agree satisfactorily with Bitter's varietal segregates.

Tristan: *Carmichael* s.n. (BM), s.n. (K); *Dickson* 117 (BM); *Dyer* 3549 (PRE, NBG, BM, K, O); *Fleming* 82 (E); *Glass* s.n. (BM); *Keytel* 1797 (NBG, K, BM): s.n. (PRE [herb. Marloth 4719]); *Macgillivray* 355 (K), s.n. (BM); *Mejland* 345 (O, BM, PRE); 641 (O); 815 (O); *Milne* s.n. (K); *Moseley* s.n. (K. BM); *Rogers* 6 (BM); *Stableford* 57 (BM); *Thouars* s.n. (P -holotype of *Ancistrum sarmentosum*, BM); *Wace* T.68 (BM). **Inaccessible:** *Christophersen* 2552 (O, BM); *Moseley* s.n. (K, BM, E—all isotypes of var. *longiuscula*) *Stableford* 124 (BM); *Wilkins* 69 (BM). **Nightingale:** *Christophersen* 2090 (BM), 2090b (O), 2106 (O); *Fleming* 63 (E); *Moseley* 17 Oct. 1873 s.n. (K, BM -syntypes of var. *lusciniae*) Oct. 1873 s.n. (BM, E -syntypes of var. *lusciniae*) *Stableford* 3 (K), s.n. (K). **Gough:** *Discovery 'W.S' Exped.* s.n. (BM); *Fleming* 19 (E); *van de Merwe* 34 (PRE); *Wace* 60 (BM, PRE), 77 (BM).

Acaena stangii Christoph.

Endemic. First discovered by Christophersen on Tristan da Cunha in January 1938 growing in *Empetrum* heath and described by him as new (Christophersen, 1944: 7–10). He considers this species to be more related to the Australian forms of *Acaena* than to those from South America.

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* Bitter designates the holotype of this variety as being in the herbarium at Stockholm but fails to cite a collection.

Tristan: *Bonomi* s.n. (NBG [herb. Mus. Austro-Afric. 1141]); *Christophersen* 46 (O, BM), 831 (O -holotype, BM), 1271 (O, BM); *Dickson* 112 (BM, AAS); *Mejland* 632 (O), 814, (O); *Wace* T.13 (BM), T.69 (BM). **Inaccessible:** *Christophersen* 2360 (O), 2581 (O, BM). **Gough:** *Wace* 81 (BM), 107 (BM).

Malus sylvestris subsp. **mitis** (Wallr.) Mansf.

Introduced. Wace & Holdgate (1976: 45) report that on Tristan da Cunha apples have been widely planted around the island at low altitude but do not appear to be spreading. A few trees at Stony Beach (Crawford, 1941: 48) were known to have been there as least earlier than 1937. Apples have also been reported on Inaccessible Island, where a few were found amongst *Spartina* tussock at Saltbeach and Blenden Hall (Wace & Dickson, 1963: 333).

Tristan: *Fleming* 54 (E).

Prunus persica (L.) Batsch

Introduced. Herbarium material collected on Tristan da Cunha during the 1937–38 Norwegian Scientific Expedition at both Sandy Point and between Hagan Point and Miller Point came from stunted trees, probably originating from stock planted by early settlers.

Tristan: *Christophersen* 422 (O, BM); *Mejland* 1173 (O, BM).

Rosa rubiginosa L.

Probably introduced. Collected on Tristan da Cunha in 1937 in a gorge on the road to the Potato Patches.

Tristan: *Mejland* 154 (O, BM).

Rosa spinosissima L.

Probably introduced. Collected on Tristan da Cunha in February 1904 but without precise locality.

Tristan: *Bonomi* 15 (NBG [herb. Mus. Austro-Afric. 1140]).

Rubus saxatilis L.

Introduced. First noted on Tristan da Cunha by Mrs Barrow, who refers to the presence of blackberry as being 'scanty' (Barrow, 1910: 177). In 1937 Christophersen collected it in a pasture on Hill Piece. Wace reports that blackberries now grow quite well, particularly at Sandy Point (Wace & Holdgate, 1976: 45).

Tristan: *Christophersen* 1330 (O).

CRASSULACEAE

Crassula pellucida L.

Introduced. First found on Tristan da Cunha by Stableford during the summer of 1954 by a stream or 'watron' near the Settlement.

Tristan: *Stableford* 1 (BM), s.n. (K); *Wace* T.63 (BM).

CALLITRICHACEAE

Callitriche christensenii Christoph.

Endemic. Originally described from material collected on Gough Island by Christensen in 1933, although specimens gathered there nearly 20 years before by R. N. R. Brown during the visit of the Scottish National Antarctic Expedition, April 1904, have since been identified as belonging to this taxon. The species has also been subsequently found on Tristan da Cunha, Inaccessible Island and Nightingale Island.

Tristan: *Christophersen* 544 (O), 1272 (O); *Dickson* 111 (BM, AAS); *Mejland* 1360 (O). **Inaccessible:** *Christophersen* 2388 (O), 2438 (O), 2560 (O). **Nightingale:** *Christophersen* 2093 (O). **Gough:** *Christensen* s.n. (O -holotype); *Brown* s.n. (K); *van der Merwe* s.n. (PRE); *Wace* 15 (BM), 79 (BM).

MYRTACEAE

Eucalyptus viminalis Labill.

Introduced. It is not known when this species was introduced on Tristan da Cunha, but Wace & Holdgate (1976: 45) report that it had thrived near the pine plantation at Sandy Point prior to 1968. Fleming collected a specimen at this locality in December 1971.

Tristan: *Fleming* 40 (E).

ONAGRACEAE

Oenothera indecora subsp. **bonariensis** Dietr.

Introduced. Recorded on Tristan da Cunha by Stableford in 1953-54. Probably a garden escape.

Tristan: *Stableford* s.n. (K).

UMBELLLIFERAE

Apium australe Thouars CELERY

A. goughense Bak.f. & Wilk.

Native. First recorded on Tristan da Cunha by Aubert Du Petit-Thouars in 1793 and later frequently collected on all islands of the group. It occurs from sea-level to about 1000 m, mainly on rocks and scree slopes amongst moss and dense fern. *A. goughense,* described by Baker & Wilkins (Wilkins 1925, p. 68) and based on material collected by the latter in 1922 on Gough Island, appears to exhibit little, if any, difference in characters from some of the variations found in the polymorphic *A. australe,* and therefore I follow Christophersen (1968) in not regarding it as a distinct entity.

Tristan: *Bonomi* 18 (K, NBG [herb. Mus. Austro-Afric. 1138]); *Carmichael* s.n. (BM, K); *Christophersen* 25 (BM, O) 427 (O, BM), 445 (O, BM), 635 (O, BM), 1020 (O, BM), 1276 (O), 1277 (O), 1324 (O); *Dickson* 43 (BM, AAS); *Dyer* 3568 (PRE, NBG, K); *Keytel* 1800 (NBG, K, BM), s.n. (PRE [herb. Marloth. 4723]); *Mejland* 1591 (O), 1636 (O, BM,) 1637 (O, BM); *Moseley* s.n. (K); *Rogers* (BM); *Thouars,* s.n. (P -holotype of *A. australe*); *Wace* T.73 (BM). **Inaccessible:** *Christophersen* 2419 (O, BM), 2421 (O, BM), 2422 (O), 2550 (O, BM), 2551 (O), 2587 (O, BM); *Fleming* s.n. (E); *Moseley* s.n. (BM. K); *Stableford* 126 (BM), 127 (BM). **Nightingale:** *Christophersen* 2007 (O, BM), 2045 (O), 2046 (O, BM), 2065 (O), 2135 (O), 2182 (O, BM); *Stableford* 76 (BM), s.n. (K). **Middle:** *Christophersen* 2026 (O, BM), 2027 (O), 2028 (O). **Stoltenhoff:** Christophersen 2149 (O). **Gough:** *Brown* s.n. (K, E); *Christensen* s.n. (O, BM); *Fleming* 16 (E); *MacMillan* s.n. (PRE); *van der Merwe* 45 (PRE), 58 (PRE, K): *Wace* 34 (BM) 89 (BM), 117 (BM); *Wilkins* 82 (BM), 83 (BM), & 84 (BM-synotype of *A. goughense).*

Centella asiatica (L.) Urban*

Hydrocotyle asiatica L.

Introduced. So far only recorded from Tristan da Cunha, where the first specimen was collected by Bonomi in 1904. Occasionally found in short grass of gardens, pasture and waste ground near the Settlement, at the Potato Patches, and also near Jenny's Watron.

Tristan: *Bonomi* s.n. (NBG [herb. Austro-Afric. 1137]); *Christophersen* 16 (O), 269 (O); *Dickson* 89 (BM, AAS); *Dyer* 3537 (PRE, NBG); *Keytel* 1799 (NBG); *Mejland* 105 (O) 349 (O, BM); *Stableford* 8 (BM), 98 (BM), 113 (K); *Wace* T.54 (BM), T.90 (BM).

Hydrocotyle capitata Thouars

Native. First collected on Tristan da Cunha by Aubert Du Petit-Thouars in 1793. Since then the species has been found on the island several times, and occurs not uncommonly in 'grassy places from the lowlands to middle altitudes' (Christophersen, 1968: 15). It has been found between rocks on Stag Beach and also in a small valley bog amongst moss at Jenny's Watron. It also occurs on Inaccessible and Gough Islands in similar damp situations, although it has not yet been noted from Nightingale Island. It has never been recorded growing wild outside the group.

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* A 1962 record of this species on Inaccessible Island attributed to Dickson is given in Wace & Dickson (1965, Appendix A), but no specimen has been traced to substantiate it.

Tristan: *Carmichael* s.n. (BM, K); *Christophersen* 11 (O, BM), 550n (O), 1241 (O), 1560 (O); *Dickson* 96 (BM, AAS); *Dyer* 3538 (PRE, NGB, K), 3566 (PRE, NBG, K); *Keytel* 1798 (NBG, K); *Macgillivray* 356 (K); *Mejland* 107 (O), 621 (O, BM), 1152a (O, BM), 1428 (O, BM); *Moseley* s.n. (K); *Rogers* s.n. (K); *Siggeson* 45 (O); *Stableford* 31 (BM), 100 (BM), s.n. (K); *Thouars* 95 (P -holotype, BM); *Wace* T.55 (BM). **Inaccessible:** *Christophersen* 1279 (O), 2325 (O), 2579 (O); *Fleming* s.n. (E); *Moseley* s.n. (BM, K). **Gough:** *Brown* s.n. (K, E); *Discovery 'W.S.' Exped.* s.n. (BM); *van de Merwe* 3 (PRE, K); *Wace* 50 (BM), 126 (BM); *Wilkins* 74 (BM); *Christensen* s.n. (O) from Gough Island probably also belongs to this species.

RUBIACEAE

Galium aparine L.

Introduced. First found on Tristan da Cunha in December 1937 in a garden at the Settlement, where it occurred as a weed.

Tristan: *Christophersen* 407 (O); *Mejland* 1294 (O, BM).

Nertera assurgens Thouars

Endemic. First found on Tristan da Cunha by Aubert Du Petit-Thouars in 1793, the type being described by him and based on his own material (Aubert Du Petit-Thouars 1808; 42). Since then it has been collected several times on the island, where it usually grows in moss in damp localities between 150 and 650 m. It has been found once on Inaccessible Island, but the recent record by Stableford from Nightingale Island is probably an error for Tristan da Cunha (see footnote).

Tristan: *Carmichael* s.n. (BM, K); *Christophersen* 458 (O, BM, PRE), 1722 (O); *Dickson* 12 (BM, AAS); *Fleming* 68 (E); *Keytel* 1801 (NBG, K); *Mejland* 1634 (O, BM), 1725 (O, BM), 1731 (O); *Stableford* 17* (K), 61 (BM); *Thouars* s.n. (P -holotype, BM); *Wace* T.30 (BM). **Inaccessible:** *Moseley* s.n. (BM).

Nertera depressa Banks & Sol. ex Gaertn. FOWLS'S BERRY BUSH; CHICKEN BERRY

N. granadensis (L.f.) Druce

Native. First found on Tristan da Cunha by Aubert Du Petit-Thouars in 1793. This small, creeping plant, rooting at the nodes, forms dense patches amongst grass and was in 1937 reported by Dyer (1939: 605) as being 'frequent on the margin of the Settlement plateau towards the landing beach'. It also occurs up the mountain slope, where during the same expedition Dyer found it 'often with numerous little red berries'. It has also been found on Inaccessible, Nightingale and Gough Islands.

Tristan: *Bonomi* 17 (K, NGB [herb. Mus. Austro-Afric. 1124]); *Carmichael* s.n. (BM, K); *Christophersen* 7 (O, BM), 62 (O), 550h (O); *Dyer* 3539 (PRE, NBG, K), 3581 (NBG, K); *Fleming* 88 (E); *Glass* s.n. (BM); *Mejland* 136 (O), 1732 (O); *Moseley* s.n. (K); *Rogers* 16 (BM), s.n. (K); *Siggeson* 46 (O)†; *Stableford* 62 (BM); *Thouars* s.n. (P); *Wace* T.6 (BM), T.64 (BM), T.70 (BM). **Inaccessible:** *Christophersen* 2549 (O, PRE). **Nightingale:** *Christophersen* 2040 (O); *Fleming* 65 (E), s.n. (E). **Gough:** *Brown* s.n. (K, E); *Discovery 'W.S.' Exped.* s.n. (BM); *Fleming* 32 (E); *Wace* 61 (BM), 111 (BM), 129 (BM), 149 (BM).

Christophersen (1944: 12) has described a forma **fimbriata** which he states as differing from the typical form in having the cells of the callose margins to the leaves developed into papillae and hairs. It is not possible to say how widespread this form may be until a critical examination can be made on all material collected so far from Tristan da Cunha and from the other islands. Material collected during the Norwegian Scientific Expedition 1937–38 which Christophersen has assigned to this form is as follows:

Tristan: *Mejland* 344 (O), 1374 (O, BM), 1388 (O -holotype of *f. fimbriata* BM), 1619 (O), 1632 (O, BM), 1633 (O), 1638 (O), 1723a (O), 1724 (O, BM), 1726 (O), 1727 (O), 1728 (O, BM), 1729 (O), 1730 (O), 1733 (O), 1734 (O, BM), 1761 (O, BM, PRE), 1771 (O, BM), 1817 (O).

Nertera holmboei Christoph.

Endemic. Described as a new species by Christophersen (1944: 13–14) from a specimen collected by him amongst tussock in a rocky place on Middle Island, February 1938, during the Norwegian Scientific Expedition to Tristan da Cunha 1937–38. The earliest known record for the group however is a specimen collected by Moseley on Inaccessible Island on 16 October 1873 during the HMS *Challenger Expedition.* He also found it the following day on Nightingale Island. Besides the above mentioned islands it has also been recorded on Stoltenhoff Island. It favours shady moist places, amongst mosses. Christophersen (loc. cit.) states that it is distinguished by its large, broadly ovate to reniform leaves with even margins and by its large fruits (up to 6 mm in diameter) with seeds up to 3.3 mm long.

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* The label accompanying this gathering gives Nightingale Island as the locality, but most probably the specimen was collected on Tristan da Cunha.

† Not seen by me in Oslo herbarium in October 1973, but cited as being there by Christophersen (1937).

Inaccessible: *Christophersen* 2476 (O, BM); *Dickson* 132 (BM, AAS); *Moseley* s.n. (K). **Nightingale:** *Christophersen* 2103 (O, BM); *Dickson* 138 (BM, AAS); *Moseley* s.n. (K). **Middle:** *Christophersen* 2021 (O -holotype, BM). **Stoltenhoff:** *Christophersen* 2148 (O).

COMPOSITAE

Anthemis cotula L.

Introduced. First collected on Tristan da Cunha in 1904 by Bonomi. It has been found near the Settlement as a weed of cultivation.

Tristan: *Bonomi* 10 (NBG [herb. Mus. Austro-Aric. 1133]); *Keytel* 1815 (NBG, BM); *Mejland* 1292 (O, BM).

Bellis perennis L.

Introduced. Originally collected on Tristan da Cunha by Mejland in 1937 near the Settlement. It particularly favours path-sides and trampled turf. Double forms have been noted.

Tristan: *Mejland* 122 (O, BM); *Siggeson* 37 (O); *Wace* T.91 (BM).

Chevreulia sarmentosa (Pers.) Blake

C. stolonifera Cass.; *Xeranthemum caespitosum* Thouars

Native. First collected on Tristan da Cunha in January 1793 by Aubert Du Petit-Thouars whose material became the type of his *Xeranthemum caespitosum.* It has been found on the island on several occasions, growing in both pasture and meadow and also in the short turf near the cliff edge west of the Settlement. The species has also been recorded for Inaccessible Island during the Norwegian Expedition of 1937-38.

Tristan: *Bonomi* 8 (NGB [herb. Mus. Austro-Afric. 1134], K); *Carmichael* s.n. (BM, K); *Christophersen* 1129 (O): *Dickson* 39 (BM, AAS); *Mejland* 1104 (O, BM), 1165 (O), 1664 (O); *Siggeson* 52 (O); *Stableford* 94 (BM); *Thouars* s.n. (P[*] -holotype of *X. caespitosum,* BM); *Wace* T.84 (BM). **Inaccessible:** *Christophersen* 2575 (O, BM).

Conyza sumatrensis (Retz.) E. H. Walker

C. floribunda Kunth

Introduced. First collected on Tristan da Cunha by Mejland near the Settlement in 1938, and since found several times on the island in a few other localities.

Tristan:[†] *Christophersen* 1787 (O); *Dickson* 14 (BM), 178 (BM); *Mejland* 1296 (O), 1476 (O, BM), 1645 (O, BM); *Stableford* 21 (BM), s.n. (K).

Cotula australis (Sieber ex Sprengel) J. D. Hook.

Introduced. First found on Tristan da Cunha by both Macgillivray and Milne during the visit of HMS *Herald* in November 1852. It has been collected on the island on several occasions since, as well as on Nightingale Island by Stableford in 1954. It is a plant of open grassy places.

Tristan: *Christophersen* 1130 (O, BM); *Dickson* 34 (AAS), 86 (BM); *Dyer* 3528 (PRE, BM); *Macgillivray* s.n. (K); *Mejland* 108 (O), 126a (O), 1308 (O); *Milne* s.n. (K); *Stableford* 6 (BM), 101 (BM), s.n. (K); *Wace* T.60 (BM). **Nightingale:** *Stableford* 74 (BM), s.n. (K).

Cotula goughensis R. N. R. Brown

Endemic. Recognised as a new species by R. N. R. Brown (1905: 242, plate 9) from material he collected on Gough Island during the visit of the Scottish National Antarctic Expedition in April 1904. In later visits by Wilkins in 1922 and by Wace in 1955 the species was found to be common and widely dominant at lower levels, decreasing with altitude.

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[*] Not located by me at P in September 1975.

[†] Some of the Tristan gatherings have been identified as *Conyza bonariensis* (L.) Cronq., but all material I have seen has proved to be *C. sumatrensis.*

Gough: *Brown* s.n. (K, E—both syntypes); *Christensen* s.n. (O); *Fleming* 37 (E); *van der Merwe* 31 (PRE); *Wace* 3 (BM); *Wilkins* 78 (BM), 79 (BM).

Cotula moseleyi Hemsley

Endemic. Reported only from Nightingale Island (Fig. 20), where it was first found by Moseley during the visit of HMS *Challenger* in October 1873. It grows abundantly in damp meadows and tussock grassland.

Nightingale: *Christophersen* 2104 (O, BM), 2168 (O, BM), 2236 (O); *Dickson* 140 (BM); *Fleming* 59 (E); *Moseley* s.n. (K -holotype, BM); *Stableford* 75 (BM), s.n. (K).

Crepis capillaris (L.) Wallr.

Introduced. First collected on Tristan da Cunha near the Settlement by Dickson in February 1962.

Tristan: *Dickson* 106 (BM).

Gnaphalium candidissimum Lam.

Introduced. This species, amongst others, is stated in a recent paper by Wace & Holdgate (1976: 45) as being 'characteristic of waste ground in and around the Settlement' on Tristan da Cunha. No herbarium material for G. *candidissimum* has been seen from the island, although possibly it was collected there by Wace during his 1968 visit.

Gnaphalium luteo-album L. MUCKWEED

Introduced. First collected on Tristan da Cunha by Bonomi 1904. Common on lowland pastures and on the mountain slopes up to 1220 m. It has also been found on Inaccessible Island.

Tristan: *Bonomi* 22 (NBG [herb. Mus. Austro-Afric. 1136]); *Christophersen* 8 (O, BM); *Dyer* 3545 (PRE, NBG); *Keytel* 1803 (NBG, BM): *Mejland* 152 (O, BM), 1662 (O, BM), 1663 (O, BM); *Siggeson* 38 (O); *Stableford* 18 (BM), 95 (BM), 96 (BM), s.n. (K); *Wace* T.53 (BM). **Inaccessible:** *Christophersen* 2420 (O).

Gnaphalium purpureum L.

Introduced. First collected on Tristan da Cunha by Wace in 1955, occurring in cultivated ground around the Settlement and occasionally on lower slopes.

Tristan: *Dickson* 107 (BM); *Wace* T.61 (BM).

Gnaphalium thouarsii Sprengel COW PUDDING GRASS

G. pyramidale Thouars, non Berg.

Endemic. First collected on Tristan da Cunha by Aubert Du Petit-Thouars in January 1793 and subsequently also on Inaccessible, Nightingale and Gough Islands. It commonly occurs in wet stream gullies and on open grassy areas.

Tristan: *Carmichael* s.n. (BM); *Christophersen* 420 (O), 513 (O), 547 (O, BM), 1329 (O); *Fleming* 70 (E); *Mejland* 612 (O), 643 (O, BM), 1161 (O), 1669 (O, BM), 1670 (O, BM); *Milne* s.n. (K); *Moseley* s.n. (K); *Rogers* 18 (BM); *Stableford* s.n. (K); *Thouars* s.n. (P -holotype, BM). **Inaccessible:** *Christophersen* 2358 (O, BM), 2400b (O), 2616 (O); *Moseley* s.n. (K, BM); *Stableford* 128 (BM); *Wilkins* 67 (BM). **Nightingale:** *Christophersen* 2041 (O, BM), 2212 (O); *Stableford* s.n. (K). **Gough:** *Brown* s.n. (K, E); *Discovery 'W.S.' Exped.* s.n. (BM); *Fleming* 3 (E); *van der Merwe* 39 (K); *Wace* 14 (BM), 69 (BM), 86 (BM); *Wilkins* 85 (BM).

Hypochoeris glabra L.

Introduced. Reported only from Tristan da Cunha, where the earliest collection was made by Moseley in October 1873. It has been found as a ruderal of cultivated ground and in short turf near the Settlement, and also at the Potato Patches.

Tristan: *Dickson* 40 (BM); *Keytel* 1818 (NBG); *Mejland* 308 (O, BM), 348 (O), 1010 (O, BM); *Moseley* s.n. (BM, K); *Stableford* 27 (BM), s.n. (K); *Wace* T.57 (BM).

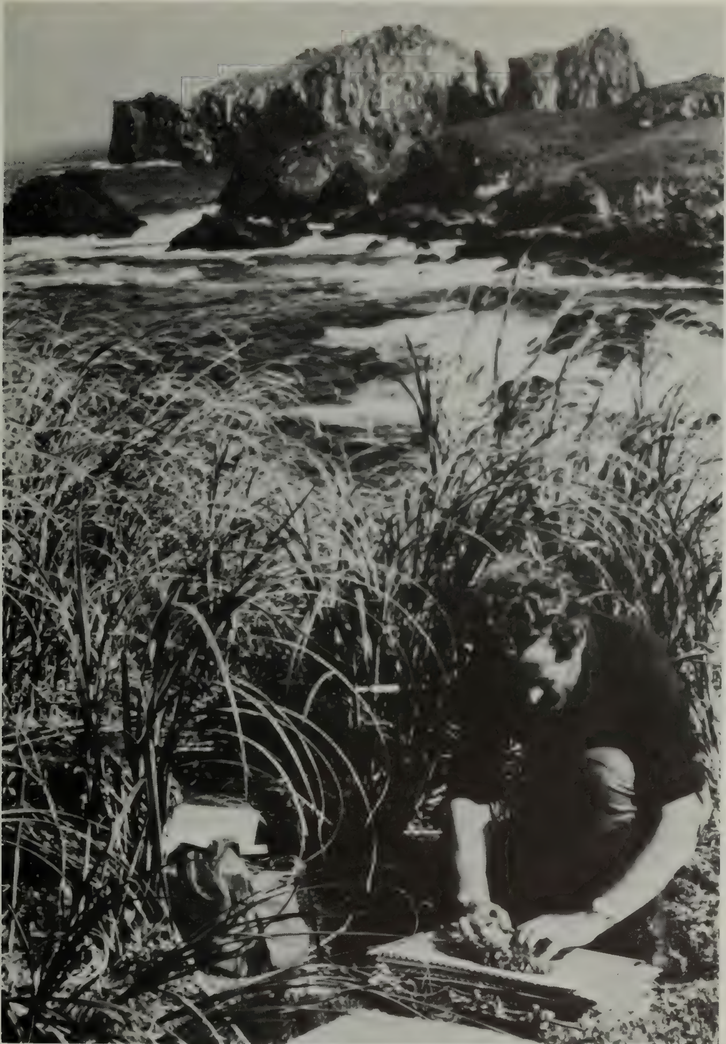

Fig. 20 N. M. Wace collecting *Cotula moseleyi* and *Apium australe* amid shoulder-high tussock grassland above Petrel Bay, north side of Nightingale Island. Middle Island, with Stoltenhoff Island beyond, form the background. November 1976. Photograph: C. D. Ollier.

Lactuca serriola L.

L. scariola L.

Introduced. This weed of cultivation was noted by Aubert Du Petit-Thouars on Tristan da Cunha in 1793 and reported in his list (Aubert Du Petit-Thouars, 1808: 46) under the name *L. sativa* L. It has not, as far is known, been subsequently recorded from the island.

Tristan: *Thouars* s.n.*

Lagenophora nudicaulis (Commerson) Dusén

L. commersonii Cass.

Native. First found on Tristan da Cunha in 1793 by Aubert Du Petit-Thouars who recorded it in his list (Aubert Du Petit-Thouars, 1808: 40) under the name *Calendula pusilla.* It grows in damp boggy places particularly amongst *Sphagnum.*

Tristan: *Christophersen* 24 (O), 49 (O), 76 (O, PRE) 550m (O); *Dickson* 31 (BM, AAS); *Dyer* 3569 (PRE); *Mejland* 623 (O), 1175 (O); *Stableford* 2† (K); *Thouars* s.n. (P). **Inaccessible:** *Christophersen* 2491 (O). **Gough:** *Wace* 73 (BM), 119 (BM).

Leontodon taraxacoides (Vill.) Mérat

Introduced. This species was collected on Tristan da Cunha during 1955–56.

Tristan: *Stableford* 97 (BM).

Leucanthemum vulgare Lamb.

Chrysanthemum leucanthemum L.

Introduced. First collected on Tristan da Cunha by Bonomi in February 1904. The species frequently occurs not only in the lowland pasture, but also on semi-stabilised ground, boulder scree, and in rock crevices. It has also been found as a weed at the Potato Patches.

Tristan: *Bonomi* 9 (NBG [herb. Mus. Austro-Afric. 1135]); *Dyer* 3544 (PRE, NBG); *Keytel* 1816 (NBG, BM); *Mejland* 350 (O, BM); 1436 (O, BM), 1452 (O, BM), 1646 (O, BM), *Rogers* 9 (BM); *Stableford* 30 (BM), s.n. (K), *Wace* T.23 (BM).

Senecio vulgaris L.

Introduced. This species has been found as a weed on Tristan da Cunha both at the Settlement and at the Potato Patches. It was first collected on the island by Moseley in October 1873.

Tristan: *Christophersen* 404 (O, BM); *Dyer* 3527 (PRE, NBG); *Keytel* 1814 (NBG, BM); *Mejland* 128 (O), 170 (O); *Moseley* s.n. (BM); *Stableford* 28 (BM), s.n. (K).

Sonchus asper (L.) Hill

Introduced. First found on Gough Island by van der Merwe in January 1957, when he stated on his label to the herbarium specimen that it was 'common inland'. It has been subsequently found on Tristan by Dickson near the Settlement in February 1962.

Tristan: *Dickson* 104 (BM). **Gough:** *van der Merwe* 49 (PRE).

Sonchus oleraceus L.‡

Introduced. The earliest collection was made on Tristan da Cunha by Carmichael in 1817; in 1962 Dickson noted that it was common throughout the island. It has been found on all six islands of the group.

Tristan: *Bonomi* s.n. (NBG [herb. Mus. Austro-Afric. 1132]); *Carmichael* s.n. (BM); *Christophersen* 3 (O); *Dickson* 105 (BM); *Keytel* 1802 (NBG, K); *Mejland* 114 (O, BM), 132 (O, BM), 172 (O), 1150 (O, BM), 1554 (O, BM); *Moseley* s.n. (K); *Stableford* s.n. (K); *Wace* T.89 (BM). **Inaccessible:** *Christophersen* 2617 (O); *Fleming* s.n. (E); *Moseley* s.n. (BM, K). **Nightingale:** *Christophersen* 2107 (O), 2109 (O). **Middle:** *Christophersen* 2023 (O). **Stoltenhoff:** *Christophersen* 2150 (O). **Gough:** *Brown* s.n. (K, E—wrongly labelled as *Hypochaeris glabra); Christensen* s.n. (O); *Wace* 10 (BM).

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* No specimen could be found when I searched for it in the Paris Herbarium in September 1975.

† The label on the Kew sheet gives the locality as Nightingale, but this is probably in error for Tristan (see remarks under Stableford, p. 352).

‡ There exists in K a gathering of another *Sonchus* collected by R. N. R. Brown during the visit of the Scottish National Antarctic Expedition to Gough in 1912 which may be *S. asper* or even *S. arvensis,* but as the single specimen is juvenile and sterile its identity cannot be determined.

CAMPANULACEAE

Lobelia erinus L.
Introduced. The earliest collection is that of Stableford in 1954 on Tristan da Cunha where it is now a common weed of open cultivated ground around the Settlement and Mission Garden.

Tristan: *Stableford* 13 (BM), s.n. (K); *Wace* T.56 (BM).

EMPETRACEAE

Empetrum rubrum Vahl TRISTAN CRANBERRY

E. nigrum var. *rubrum* (Vahl) Hemsley; *E. medium* Carmich.

Native. First collected on Tristan da Cunha by Aubert Du Petit-Thouars in 1793 and since then found on all the islands of the group except Middle Island, although in all probability it also occurs there. It is commonly found associated with in the *Blechnum/Phylica* heath on the lower slopes and as a creeping ecotype on upper scree slopes. Fascinated specimens are not uncommon. In addition to the type, two other forms and one variety have been recognized from the Tristan-Gough group by some workers: the forma **medium** (Carmich.) Good (Good, 1927: 517) has narrower leaves with distinctly apiculate tips; the forma **pulvinatum** Christoph. (Christophersen, 1944: 11–12, and Christophersen, 1968: 19) being of a cushion-like habit and has glabrous leaves, only a few of which can be characterized as subspathulate; and the var. **tristanitorum** Christoph. (Christophersen, 1944: 10–11, and Christophersen, 1968: 18) distinguished by 'its prostrate matted habit, the shape of its long, narrowly elliptic leaves, lanceolate or oblanceolate rarely truly elongate, and large, light-red, shining translucent berries, sweet to the taste' (cf. the smaller sour-tasting fruit of the type). This variety **tristanitorum** is said to grow at high altitudes (from about 1000 m. up to the Peak) and is relished by the Tristanites who call the fruits 'Peak Berries' (Christophersen, 1968: 18). However, it seems that these forms and the variety are of doubtful validity, as *E. rubrum* from the islands, as elsewhere, exhibits a wide degree of polymorphism.

Tristan: *Bonomi* 19 (PRE), s.n. (NBG [herb. Mus. Austro-Afric. 1125]); *Christophersen* 1 (O, BM), 414 (O, BM), 530 (O, BM), 1031 (O); *Dickson* 121 (BM, AAS); *Dyer* 3520 (PRE), 3548 (PRE, NBG), 3567 (PRE, NBG); *Fleming* 79 (E), 84 (E), 92; (E) *Keytel* s.n. (PRE [herb. Marloth 4722]); *Mejland* 1011 (O, BM), 1012 (O, BM), 1138 (O); *Rogers* 8 (BM); *Siggeson* 39 (O); *Stableford* 56 (BM), 99, (BM); *Thouars* s.n. (P); January 1877 [no collector] 15 (BM). **Inaccessible:** *Christophersen* 2497 (O, BM), 2546 (O, BM), 2597 (O); *Wilkins* 42b (BM). **Nightingale:** *Christophersen* 2033 (O, BM), 2095 (O, BM); *Moseley* s.n. (BM). **Stoltenhoff:** *Christophersen* 2153 (O). **Gough:** *Brown* s.n. (E); *Fleming* 5 (E), 34 (E); *van der Merwe* 35 (PRE); *Wace* 35 (BM).

Herbarium material recognised by certain workers as belonging to the forms and variety mentioned above is as follows:

forma **medium** (Carmich.) Good

Tristan: *Carmichael* s.n. (BM -holotype); *Macgillivray* s.n. (BM); *Moseley* s.n. (BM); *Wace* T.43 (BM). **Gough:** *Wace* 71 (BM).

forma **pulvinatum** Christoph.

Tristan: *Christophersen* 31 (O -holotype, BM), 630 (O), 1128 (O), 1380 (O); *Mejland* 1715 (O).

var. **tristanitorum** Christoph.

Tristan: *Christophersen* 628 (O, BM), 629 (O), 1745 (O -holotype, BM), 1779 (O); *Mejland* 1359 (O); *Wace* T.47 (BM). **Gough:** *Wace* 109 (BM), 125 (BM).

PRIMULACEAE

Anagallis arvenis L.
Introduced. First cited (but without reference to a collector) for Tristan da Cunha by Hemsley (1885, Pt.II: 145) as being 'among introduced plants more or less established'. The

part of his account relating to this island (loc. cit.) was based on the collection of Moseley, together with the earlier material of Carmichael and Macgillivray. No specimen has been traced in any of the extant specimens of these collectors in the herbaria at BM, K or E. The earliest gathering seen, made by Keytel in 1908–09, exists in K. *Anagallis arvensis* has now become frequent as a weed of cultivation and occurs in waste places, both around the Settlement and at the Potato Patches.

Tristan: *Christophersen* 287 (BM, O); *Keytel* 1811 (NBG, K); *Dickson* 108 (BM); *Mejland* 304 (O); *Stableford* 16 (BM), s.n. (K).

BORAGINACEAE

Lithospermum sp.

Introduced. Reported for Tristan da Cunha by Christophersen (1937: 10), based on a single gathering made by Siggeson in November 1934. Christophersen (loc. cit.) states that he was 'unable to match it with any known species of this genus'. No further material has since been discovered on the island.

Tristan: *Siggeson* 48 (O)*.

Myosotis discolor Pers.

Introduced. First collected on Tristan da Cunha in 1937. It has been found near the Settlement, where in 1955 it was noted to be common in pastures, and at the Potato Patches.

Tristan: *Christophersen* 403 (O, BM); *Dickson* 84 (BM); *Mejland* 125 (BM), 128b (O), 176 (O, BM); *Stableford* 12 (BM), 107 (BM), 118 (BM), s.n. (K); *Wace* T.58 (BM).

CONVOLVULACEAE

Calystegia sepium subsp. **americana** (Sims) Brummitt†

Native. First collected on Tristan da Cunha in 1908–09 by Keytel who remarked that it was 'not uncommon'. Since that time it has been found at several localities on that island, e.g. around the Settlement, and at Stony Beach, Sandy Point, Anchorstock Bay and at the Potato Patches. It has also been collected on Inaccessible Island. The comparatively large corollas (50–60 mm long) are pale pink or violet-pink in colour.

Tristan: *Christophersen* 299 (O, BM), 447 (O, BM); *Mejland* 1135 (O, BM), 1407 (O), 1413 (O, BM); *Keytel* 1809 (NBG, K, BM); *Stableford* 26 (BM), s.n. (K). **Inaccessible:** Skjelten in *Christophersen* 2346 (O, BM); *Christophersen* 2576 (O, BM), 2599 (O, BM); *Dickson* 131 (BM).

Calystegia tuguriorum (G. Forster) R.Br. ex J. D. Hook.

Probably native. A specimen collected on Inaccessible Island by Christophersen in February 1938, during the Norwegian Scientific Expedition of 1937–38, has recently been recognized as this well known amphi-Pacific species (Brummitt & Groves, 1981). Unfortunately the specimen collected was sterile, so material with flowers and fruit is desired. The corollas of *C. tuguriorum,* which may be white or pink, are usually smaller than those of *C. sepium* subsp. *americana,* being 25–35 mm long. *C. tuguriorum* has a distribution from New Zealand, through Chatham Island and Masafuera (Juan Fernandez islands) to the Valdivia and Chiloe provinces of Chile.

Tristan: *Christophersen* 2147 (BM).

Calystegia soldanella R.Br.

Native. First found on Tristan da Cunha in 1816–17 by Carmichael, who remarks that it occurs on the south-east side of the island, growing in the sand close to the shore, restricted to a single area. It appeared to be of recent introduction (Carmichael, 1819: 505). Unfortunately no material can be traced of any specimen gathered by him at this locality. A sheet collected nearly a hundred years later by Bonomi in February 1904 exists in NBG, and since then the species has been found on several occasions, all on fixed sand and mostly on the island's beaches.

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* The herbarium material of this gathering was not traced in O during my visit in October 1973.

† Moseley (1874: 380) mentions that on Inaccessible Island he observed a convolvulus that was 'very abundant on the cultivated ground near their hut' [of two Germans] (the brothers Stoltenhoff who had been there for two years fur-sealing—see p. 341 under Stoltenhoff Island). There is no herbarium material of this plant in Moseley's collection at K, but the plant is more likely to have been a *Calystegia* than a *Convolvulus* sens. str.

Tristan: *Bonomi* 24 (K), s.n. (NBG [herb. Austro-Afric. 18626]); *Dickson* 5 (BM); *Keytel* 1808 (NBG, BM); *Mejland* 164 (O, BM), 1408 (O, BM); *Stableford* 120 (BM).

SOLANACEAE

Physalis peruviana L.
Introduced. The inclusion of this taxon in the alien flora of the Tristan-Gough group is based on a single record of a specimen found by Christophersen on Inaccessible Island in 1938.

Inaccessible: *Christophersen* 2598 (O, BM, K).

Solanum nigrum L. TRISTAN BLACKBERRY
Introduced. First collected on Tristan da Cunha by Keytel 1909–09, and since then it has become a common weed around the Settlement. It has also been found on Inaccessible Island where it was gathered during the visit of the Norwegian Scientific Expedition in Febrauary 1938. Christophersen (1968: 21) remarks that 'some of the plants are distinctly woody at the base, as is frequently the case in warmer regions'.

Tristan: *Dickson* 103 (BM, AAS); *Keytel* 1807 (NBG, BM); *Mejland* 1291 (O); *Rogers* 14 (BM); *Stableford* s.n. (K). **Inaccessible:** *Christophersen* 2302 (O, K), 2324 (O, BM), 2418 (O).

SCROPHULARIACEAE

Verbascum virgatum Stokes
Introduced. First collected on Tristan da Cunha by Keytel in 1908–09. Since that date it has been found several times, mainly around the Settlement near gardens.

Tristan: *Christophersen* 1741 (O), 1783 (O); *Dickson* 83 (BM); *Mejland* 1300 (O), 1405 (O), 1451 (O, BM); *Keytel* 1820 (NBG, K).

Veronica agrestis L.
Introduced. Originally collected by Mejland on Tristan da Cunha in March 1938. It occurs at the Settlement by paths and as a weed of gardens.

Tristan: *Dickson* 73 (BM), 145 (BM); *Mejland* 1435 (O, BM).

Veronica serpyllifolia L.
Introduced. First collected on Tristan da Cunha by Keytel in 1908–09. It occurs commonly both in damp places all over the island and in pastures near the Settlement. Dyer (1939: 605) notes that the species was 'occasionally a pioneer colonizer along with *Plantago lanceolata* and *Cynodon dactylon*'.

Tristan: *Dickson* 38 (BM, AAS); *Dyer* 3536 (PRE, NBG, K); *Keytel* 1822 (NBG, K); *Mejland* 135 (O, BM), 1631 (O, BM); *Stableford* 18 (K*), 29 (BM), 60 (BM), 106 (BM), s.n. (K); *Wace* T.52 (BM).

VERBENACEAE

Verbena officinalis L.
Introduced. First collected on Tristan da Cunha by Bonomi in 1904. It occurs at the Settlement near gardens and in the pastures.

Tristan: *Bonomi* 21 (NBG [herb. Mus. Austro-Afric. 1130]); *Dickson* 47 (BM); *Keytel* 1821 (NBG, BM); *Mejland* 341 (O, BM); *Stableford* 3 (BM), 24 (BM), s.n. (K).

LABIATAE

Leonotis leonurus (L.) R.Br.
Introduced. This record is based on a single specimen collected on Tristan da Cunha near the Settlement in February 1938. It was probably an escape from a garden, perhaps originally as an introduction from South Africa.

Tristan: *Mejland* 1644 (O, BM).

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* Localised as from Nightingale Island but probably an error for Tristan da Cunha.

Prunella vulgaris L.
Introduced. First found on Tristan da Cunha by Mejland in January 1938. It occurs as a weed of gardens at the Settlement, and also in damp situations at the Potato Patches.

Tristan: *Mejland* 1287 (O, BM), 1745 (O); *Stableford* 19 (BM), s.n. (K).

PLANTAGINACEAE

Plantago lanceolata L.
Introduced. First collected on Tristan da Cunha by Bonomi in February 1904. It is found in pastures around the Settlement and at the Potato Patches. Christophersen (1968: 21) remarks that during the Norwegian Scientific Expedition of 1937–38 the species was exceedingly common in the pastures of the Settlement and, in certain places, as on Hill Piece, it was the dominant plant in extensive meadows. More recently, during 1956–57, it was collected on Gough Island.

Tristan: *Bonomi* s.n. (NBG [herb. Mus. Austro-Afric. 1131]); *Christophersen* 1331a (O); *Dyer* 3546 (BM); *Keytel* 1810 (NBG, BM); *Mejland* 159 (O), 1303 (O, BM), 1655 (O, BM), 1656 (O, BM); *Rogers* 17 (BM); *Siggeson* 43 (O); *Stableford* 15 (BM), 103 (BM), 113 (BM), 193 (K); *Wace* T.83 (BM). **Gough:** *van der Merwe* s.n. (PRE [Nat. Herb. Pretoria 36478]).

Plantago major L.
Introduced. First collected on Gough Island by R. N. R. Brown in 1904, and later (between 1922–25) on Tristan da Cunha near the Settlement by the Rev. & Mrs H. M. Rogers. It has since been found on Inaccessible Island.

Tristan: *Dyer* 3531 (PRE); *Mejland* 1298 (O, BM); *Rogers* 15 (BM). **Inaccessible:** *Christophersen* 2341 (O, BM); *Stableford* 125 (BM). **Gough:** *Brown* s.n. (E); *van der Merwe* 70 (PRE); *Wace* 66 (BM).

CHENOPODIACEAE

Atriplex plebeja Carmich.
Endemic. First collected on Tristan da Cunha in 1816–17, by Carmichael who described it as a new species (Carmichael, 1819: 508). It was not collected again from the group until 1938, when during the Norwegian Scientific Expedition it was found on Nightingale, Middle and Stoltenhoff Islands. A specimen collected on Tristan da Cunha during the Royal Society Expedition of 1962 (*Dickson* 66) may possibly be this species, but the material is immature.

Tristan: *Carmichael* s.n. (K -holotype); *Dickson* 66 (BM possibly this species—see above). **Nightingale:** *Christophersen* 2108 (O); *Stableford* 77 (BM), s.n. (K). **Middle:** *Christophersen* 2019 (O). **Stoltenhoff:** *Christophersen* 2151 (O).

Chenopodium album L.
Introduced. First recorded on Tristan da Cunha in January 1793 by Aubert Du Petit-Thouars. Although, in the list of plants found during the course of his visit to the island he remarks 'J'ai trouvé quelques pieds de cette plante européene' (Aubert Du Petit-Thouars, 1808: 87), I failed to trace any specimen in P during my visit in October 1975. It does not appear to have been found again on the island by any subsequent visitor.

Chenopodium ambrosioides ISLAND TEA
subsp. **ambrosioides** var. **tomentosum** (Thouars) Aellen
C. tomentosum Thouars
Endemic variety. First found on Trista da Cunha by Aubert Du Petit-Thouars in January 1793, who described it as a new species (Aubert Du Petit-Thouars, 1808: 38); Aellen (in Christophersen, 1968: 6) considered that it was only a variety of *C. ambrosioides* subsp. *ambrosioides*. The plant has since been found on Inaccessible, Nightingale and Gough Islands. Aubert Du Petit-Thouars (loc. cit.) remarked that it was 'common everywhere' on Tristan da Cunha. and it must have still been present in quantity 90 years later for Hemsley (1885: 153) to note it as being abundant. However, continual use of this plant over the next 70 years as a substitute tea seems to have greatly diminished its occurrence.

The only locality on Tristan where Wace in 1955 noted it in any quantity was on the beach at Sandy Point. On Gough Island it grows particularly vigorously on nitrogen-rich soil around penguin rookeries.

Tristan: *Bonomi* 11 (NBG [herb. Mus. Austro-Afric. 1126]); *Carmichael* s.n. (BM, P); *Christophersen* 443 (O, BM), 1746 (O, BM); *Dickson* 67 (BM); *Glass* s.n. (BM); *Keytel* 1804 (NBG); *McCraken* s.n. (BM); *Macgillivray* 354 (K), s.n. (BM); *MacMillan* s.n. (PRE); *Milne* s.n. (K); *Moseley* s.n. (BM); *Rogers* 13 (BM), s.n. (K); *Stableford* 25 (BM), s.n. (K); *Thouars* s.n. (P -holotype, BM); *Wace* T.82 (BM). **Inaccessible:** *Christophersen* 2385 (O, BM), 2593 (O), 2620 (O, BM); *Moseley* s.n. (BM). **Nightingale:** *Christophersen* 2063* (O). **Gough:** *van der Merwe* 25 (PRE—2 sheets collected at different dates); *Wace* 92 (BM), 151 (BM), *Wilkins* 76 (BM), 77 (BM).

Chenopodium murale L.

Introduced. Originally found on Tristan da Cunha by Keytel in 1908–09 around the Settlement, but not collected since. The Kew sheet of Keytel's gathering was examined in 1929 by Paul Aellen, who thought it represented an untypical example of his var. *acutidentatum,* described originally from South Africa (Aellen 1928: 343).

Tristan: *Keytel* 1817 (NBG, K, BM).

POLYGONACEAE

Polygonum aviculare L.

Introduced. First found on Tristan da Cunha in 1937 by Dyer, who, on his label to the herbarium specimen, comments that the species was 'probably only recently introduced'. It is now a common weed around the Settlement and at the Potato Patches.

Tristan: *Christophersen* 290 (O); *Dickson* 37 (BM); *Dyer* 3529 (PRE, K); *Mejland* 1289 (O, BM); *Stableford* 9 (BM), s.n. (K).

Rumex angiocarpus Murb. SORREL DOCK; SOUR GRASS

R. acetosella subsp. *angiocarpus* (Murb.) Murb.

Introduced, now naturalised. First collected on Tristan by Macgillivray and Milne in 1852. From a study of pollen in bog peat Hafsten suggests it may have invaded Tristan da Cunha about the same time as the discovery of the island in the early 16th century, some three centuries before settlement in 1810 (Hafsten, 1951: 9 and 1960: 524). This diploid form of *R. acetosella* covers extensive meadows, often in pure stands both around the Base and on the slopes of the Peak up to 1100 m. Wace (1967: 53) considers its spread coincided with the increase in numbers of sheep on the Peak, and possibly also with that of goats and rabbits. It has also been found on Inaccessible Island.

Tristan: *Bonomi* 23 (NBG [herb. Mus. Austro-Afric. 1127]); *Christophersen* 298 (O, BM); *Dyer* 3519 (PRE, K), 3580 (PRE, NBG, K); *Fleming* 93 (E); *Keytel* 1806 (NBG, K, BM); *Macgillivray* 353a (K), 353b (K), s.n. (BM, K); *Mejland* 1545 (O, PRE), 1771a (O); *Milne* s.n. (K); *Moseley* s.n. (BM, E); *Saunders* s.n. (K); *Siggeson* 42 (O); *Stableford* 102 (BM), 112 (BM), s.n. (K); *Wace* T.45 (BM), T.59 (BM), T.67 (BM). **Inaccessible:** *Moseley* s.n. (K). **Gough:** Wace (1967: 53) reports a single plant of *R. angiocarpus* on Gough Island which inadvertently 'had been imported with some vegetables'. The plant was destroyed to prevent the possibility of it eventually invading upland areas, in the same manner as it has spread on Tristan da Cunha over the years.

Rumex crispus L.

Introduced. First found on Tristan da Cunha by Carmichael in 1817 but apparently not collected again since that date.

Tristan: *Carmichael* s.n. (BM).

Rumex frutescens Thouars PIG DOCK

R. cuneifolius Campd.

Native. First collected on Tristan da Cunha in 1793 by Aubert Du Petit-Thouars who described his material as a new species *Rumex frutescens.* Rechinger (1954: 62) stated that he could find no characters which separate *R. frutescens* (hitherto regarded as endemic to Tristan) from the polymorphic *R. cuneifolius* of South America, and in his treatment of the

South African species gave the former name in synonymy of the latter (loc. cit.: 61). However as *R. frutescens* was published eight years earlier it is therefore the valid name for the taxon, and was correctly given as such by the same author in *Flora Europaea* **1:** 85 § 22 (1964). On Tristan this species is a common lowland plant of beaches, waste ground and damp places; it also occurs on cinder scree slopes. *R. frutescens* has also been found on Inaccessible and Gough Islands, on the latter frequently on disturbed soil around penguin rookeries. As the fruits of *R. frutescens* are very buoyant, Rechinger (1954: 63) considers that its arrival in the group may well have been due to ocean currents drifting the seed from beaches along the South American coastline, where the species commonly occurs.

Tristan: *Bonomi* 12 (NBG [herb. Mus. Austro-Afric. 1129], BM); *Carmichael* s.n. (BM); *Christophersen* 6(O), 14 (O, BM, K, PRE), 829 (O, BM); *Dickson* 2 (BM); *Dyer* 3518 (PRE, NBG); *Moseley* s.n. (BM, E); *Thouars* s.n. (P -holotype); *Wace* T.93 (BM). **Inaccessible:** *Christophersen* 2573 (O, BM, K); *Fleming* s.n. (E). **Gough:** *Brown* s.n. (E); *Wace* 93 (BM).

Rumex obtusifolius L. subsp. **obtusifolius**

R. obtusifolius var. *agrestis* Fries; *R. obtusifolius* subsp. *agrestis* (Fries) Čelak

Introduced. First found on Tristan da Cunha by Bonomi in 1904. Several subspecies of *R. obtusifolius* have been described by various authors but, according to J. E. Lousley (pers. comm., 1975), only subsp. *obtusifolius* has been recorded from the Tristan-Gough islands. On Tristan the species occurs as a ruderal around the Settlement and at the Potato Patches, whilst on Inaccessible and Gough Islands it has been found on talus slopes, beaches and around elephant seal wallows and penguin rookeries.

Tristan: *Bonomi* s.n. (NBG [herb. Mus. Austro-Afric. 1128]: *Christophersen* 297 (O, BM), 902 (O, BM); *Keytel* 1813 (NBG, K); *Mejland* 115 (O, BM), 169 (O, BM): *Stableford* s.n. (K). **Inaccessible:** *Christophersen* 2596 (O), 2618 (O). **Gough:** *Brown* s.n. (K); *Christensen* s.n. (O—probably this species); *MacMillan* s.n. (PRE); *van der Merwe* 63 (PRE); *Wace* 5 (BM).

Rumex steudelii Hochst.

Introduced. Represented on Tristan by material gathered on a single occasion in a grass field at the Settlement by Mejland in January 1938. Regarding this collection, J. E. Lousley (pers.comm., 1975) provided the following remarks: 'The material collected by Mejland under No. 610 certainly belongs to the subsection *hamati,* with sharply recurved teeth on the tepals, and appears to be *R. steudelii* Hochst., which is a well known Abyssinian species. Rechinger in his monograph on the *Rumex* of Africa lists specimens from South Africa which he says are allied to *R. steudelii,* but unfortunately does not state clearly how they differ from the typical form'. Lousley further commented that the spread of this species in South Africa and also on Tristan, away from its main centre of distribution in the highlands of Ethiopia, Somalia and South-West Arabia, was probably due to the fact that seeds of members of the subsection *hamati* are easily distributed by animals and humans on account of their hooked teeth, which readily adhere to both fur and clothing.

Tristan: *Mejland* 610 (O, BM).

PIPERACEAE

Peperomia berteroana Miq. PEPPER TREE

P. tristanensis Christoph.

Possibly native. The presence of this species had been known for some time before the exact locality on Inaccessible Island was shown to E. Christophersen during the Norwegian Scientific Expedition, 1937–38. After examination of the material he collected there on 2 March 1938, Christophersen (1944: 5) considered it a new species, *P. tristanensis.* Later, however, on the basis of evidence put forward by Skottsberg (1946: 251) who compared it with the plant from the Juan Fernandez Islands, Christophersen (1968: 4) concluded that Skottsberg had established the fact that *P. tristanensis* was identical with *P. berteroana.* It is a large plant, easily recognised by its fleshy stems and dark green, glossy leaves, and was found at an altitude of 150 m above the waterfall at Salt Beach.

Inaccessible: *Christophersen* 426 (O), 502 (O), 2592 (O -holotype of *P. tristanensis*): *Glass* in *Christophersen* 1278 (O).

EUPHORBIACEAE

Euphorbia peplus L.
Introduced. A few plants were found by J. H. Dickson during the Royal Society Expedition to Tristan da Cunha, February to March 1962, in a garden at the west end of the Settlement. Obviously a weed of cultivation.

Tristan: *Dickson* 6 (BM).

MORACEAE

Ficus carica L. FIG
Introduced. A specimen was collected in a pasture at Little Sandy Gulch on Tristan da Cunha by Mejland in February 1938, no doubt representing a relict of past cultivation. Christophersen (1968: 5) states that the shoots were sterile, arising from roots that had been constantly cropped close by grazing animals.

Tristan: *Mejland* 1434 (O).

SALICACEAE

Salix babylonica L.
Introduced. Willows, probably of this species, were first mentioned in 1910 by Barrow (1910, App.: 275–277), who recorded a 'few trees on the Settlement only' on Tristan da Cunha. It has since spread to a few other localities and has also been found on Inaccessible Island. The wood of willows is used by the Tristanites for making boat ribs.

Tristan: *Christophersen* 450 (O); *Dickson* 48 (BM), 181 (BM). **Inaccessible:** *Christophersen* 2416 (O).

IRIDACEAE

Romulea rosea var. **australis** (Ewart) De Vos
Introduced. First found on Tristan da Cunha by Keytel, 1908–09, an introduction probably from South Africa. Since then it has become naturalised along roadsides and in pasture around the Settlement.

Tristan: *Keytel* 1819 (NBG, K); *Stableford* 10 (BM), s.n. (K).

LILIACEAE

Phormium tenax J. R. & G. Forster NEW ZEALAND FLAX
Introduced. First mentioned on Tristan da Cunha by Barrow (1910, Appendix: 275–277) and now locally (although extensively) cultivated in gardens near the Settlement and at the Potato Patches, being used as a wind-break (Fig. 5) and for the production of rope and string. Although it may have possibly been grown on the island earlier than the date cited above, it may not be a long standing introduction, for, as Christophersen (1968: 4) pointed out, the native tussock *(Spartina arundinacea)* had not been entirely superseded by *Phorium tenax* as a source of thatch when the Norwegian expedition visited the island in 1937–38. Wace (in litt.) states that *Spartina arundinacea* is now never used, and *Phormium tenax* only occasionally, for thatching today (Fig. 21). On Nightingale *P. tenax* has become 'the most aggressive of the aliens' now on that island, forming large clumps amongst the tussock grassland and in the *Phylica* groves and by the late 1960s 'threatened to spread all over the island, thus altering irreversibly the nesting environment of the bulk of the world population of the Great Shearwater *(Puffinus gravis)*'. Steps were therefore taken in 1968 to destroy the flax clumps, and this work is being continued by the Tristan islanders (Wace, 1976:60).

Tristan: *Christophersen* 1780 (O); *Stableford* 18 (K). **Nightingale:** No material seen.

JUNCACEAE

Juncus bufonius L.
Introduced. First collected on Tristan da Cunha by Dyer in 1937 but it is so much more abundant now, as to have become a common weed of the Settlement Plain down to the

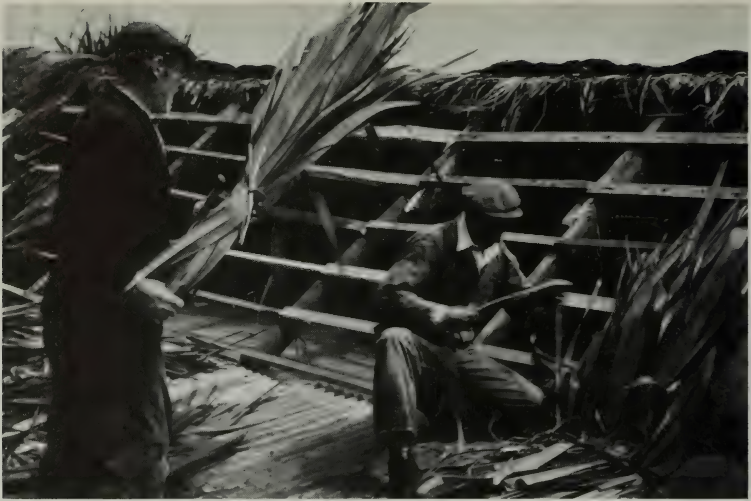

Fig. 21 Thatching one of the older cottages on Tristan da Cunha with New Zealand flax, *Phormium tenax.* George Glass holds a bundle of flax leaves ready for fixing on the roof. October 1966. Photograph: George Edwards.

beach. It has also been found at Sandy Point, 'indicating that a halophilous form is represented' (Christophersen, 1968: 3).

Tristan: *Dyer* 3524 (PRE); *Mejland* 127 (O, BM), 137 (O), 1155 (O), 1647 (O, BM, K); *Stableford* 16 (K), 51 (BM).

Juncus effusus L.

Introduced. Recorded from Tristan da Cunha at Sandy Point, first in 1938 and again in 1953–54.

Tristan: *Mejland* 1134 (O, K), 1136 (O, BM); *Stableford* 20 (K), 51 (BM), 52 (BM).

Juncus tenuis Willd.

J. macer Gray; *J. tristanianus* Hemsley

Introduced. First collected by Macgillivray on Tristan da Cunha in 1852. His material was described by Hemsley (1885: 154), as *J. tristanianus* but has since been recognised as being the same as *J. tenuis.* It occurs in wet places at the Settlement, the Potato Patches, and has also spread to the upper forest region (Christophersen, 1968: 4).

Tristan: *Christophersen* 274 (O, BM, K), 292 (O), 1268 (O); *Dickson* 101 (BM, AAS); *Dyer* 3526 (PRE, NBG); *Fleming* 81 (E); *Keytel* 1834 (NBG, K, BM); *Macgillivray* 343 (K -holotype of *J. tristanianus*); *Mejland* 116 (O, BM), 127b (O, K), 165 (O), 167b (O), 619 (O, BM, K) 620 (O), 1657 (O, BM).

Rostkovia tristanensis Christoph.

Endemic. First collected on Tristan da Cunha by Mejland in February 1938 during the Norwegian Scientific Expedition 1937–38. The material was subsequently described by Christophersen (1944: 3) as a new species, although it is closely related to *R. magellanica* of Patagonia, the Falkland Islands and New Zealand. Specimens found on Gough Island by

Wace in 1956 are also thought to be probably this species. On both islands it grows in damp upland *Empetrum* heath; on Gough it is frequent but rarely flowers.

Tristan: *Mejland* 1516 (O -holotype, BM, K). **Gough:** *Wace* 97 (BM), 132 (BM).

SCHEUCHZERIACEAE

Tetroncium magellanicum Willd.

Native. First found on Gough Island by Wace in December 1955, when it was noted as being frequent in the plateau peat of bogs at 370 m and above. No male plants were observed.

Gough: *Wace* 22 (BM), 76 (BM), 99 (BM), G.303 (K).

CYPERACEAE

Carex insularis Carmich.

Endemic. First collected on Tristan da Cunha in 1816–17, by Carmichael, who described it as new (Carmichael, 1819: 508). It has been found several times on Tristan and also on Inaccessible, Nightingale and Gough Islands. On Tristan da Cunha it is frequent amongst the tree-fern scrub at about 600 m, and on the other islands it has been found in tussock on slopes and in most places.

Tristan: *Bonomi* 3 (NBG [ex herb. Mus. Austro-Afric. 1120], K); *Carmichael* s.n. (K -holotype); *Christophersen* 33 (O, BM), 67 (O, BM, K) 216 (O), 533 (O, BM, K); *Dickson* 113 (BM, AAS); *Mejland* 1151 (O, BM, K); *Wace*, T.77 (BM), T.239 (K). **Inaccessible:** *Christophersen* 2379 (O, BM); *Moseley* s.n. (BM, K, E). **Nightingale:** *Christophersen* 2064 (O, BM, K), 2183 (O). **Gough:** *van der Merwe* 54 (K); *Wace* 6 (BM), 32 (BM), 127 (BM).

Carex thouarsii Carmich.

Endemic. First collected on Tristan da Cunha by Carmichael in 1816–17, and described as new. It has since been found on Inaccessible, Nightingale and Gough Islands. It occurs in boggy peat mostly above the tree zone, up to 760 m. A variety, var. **recurvata,** has been described by Christophersen (1944: 1), being smaller with recurved leaves.

var. **thouarsii**

Tristan: *Carmichael* s.n. (K -holotype); *Christophersen* 66 (O, BM, K), 451 (O, BM, K); *Dickson* 8 (BM), 152 (BM, AAS); *Dyer* 3752 (PRE, NBG); *Fleming* 75 (E); *Macgillivray* 337 (K); *Mejland* 636 (O); 1171 (O), 1178 (O, BM); *Stableford* 54 (BM); *Wace* T.7 (BM), T.16 (BM), T.75 (BM), T.171 (K). **Inaccessible:** *Christophersen* 2305 (O, BM, K), 2562 (O, BM, K). **Nightingale:** *Christophersen* 2035 (O, BM), 2225 (O, BM, K); *Moseley* s.n. (BM, K, E); *Wace* N.25 (K). **Gough:** *Fleming* 7 (E), 13 (E); *Wace* 53 (BM), 57 (BM), 85 (BM), 116 (BM), G.239 (K).

var. **recurvata** Christoph.

Tristan: *Christophersen* 1022 (O -holotype, BM, K); *Mejland* 1414 (O, BM), 1542 (O, BM, K), **Gough:** *Wace* 120 (BM).

Cyperus congestus Vahl OLD BULL GRASS

Mariscus congestus (Vahl) C. B. Clarke

Introduced. First collected on Tristan da Cunha by Bonomi in 1904 and recorded from several localities on the island since, including the Potato Patches. Hooper (1968: 2) considers that it may have been introduced with the advent of potato cultivation. In 1968 Wace found it colonising cinders and gravel on the side of the new volcano. It occurs also on Inaccessible Island.

Tristan: *Bonomi* 4 (K, NBG [herb. Mus. Austro-Afric. 1121]); *Christophersen* 279 (O); *Dyer* 3542 (PRE, NGB, K); *Keytel* 1850 (NBG, K, BM); *Mejland* 126 (O), 174 (O), 1174 (O); *Stableford* 53 (BM); *Wace* T.111 (K), T.117 (K), T.122 (K), T.162a (K), T.326 (K). **Inaccessible:** *Christophersen* 2483 (O, K); *Wace* I.17 (K).

Cyperus esculentus L. NEW BULL GRASS

Introduced. Collected on Tristan da Cunha by Wace in 1968. It is a very aggressive weed of the Potato Patches, where it spreads by root tubers and forms complete cover in neglected patches within a few months of the cessation of potato cultivation.

Tristan: *Wace* T.257 (K), T.162b (probably this species) (K).

Cyperus longus L. New bull grass

Probably introduced. Found on Tristan da Cunha in 1968, growing near the Settlement on a stream bank by Big Watron.

Tristan: *Wace* T.146 (K).

Cyperus tenellus L.f.

Introduced. First collected on Tristan da Cunha by Bonomi in February 1904. Like *C. congestus* and *C. esculentus,* it occurs as a weed in the Potato Patches and was probably introduced with cultivation..

Tristan: *Bonomi* 13 (K), 14 (K); *Christophersen* 221 (O, K), 405 (O, K), 1332 (O); *Mejland* 131 (O, K), 134 (O), 177b (O, K), 178 (O, K), 1422 (O), *Stableford* 32 (BM).

Scirpus bicolor (Carmich.) Sprengel*

var. **bicolor**

S. prolifer Thouars, non Rottb.; *S. thouarsianus* J. A. Schultes; *S. thouarsianus* var. *bicolor* (Carmich.) Hemsley;?*S. thouarsianus* var *pallescens* Hemsley; *Isolepis bicolor* Carmich.; *I. squarrosa* Carmich.; *S. prolifero-ramosus* Boeck.

Endemic. First collected on Tristan da Cunha by Aubert Du Petit-Thouars in 1793. Abundant in the plateau mire and wet peaty uplands on Tristan, Inaccessible, Nightingale and Gough Islands. It was reported by Dickson in 1966 to be the most successful colonist on the new volcanic material (Wace 1967: 51). On Nightingale Island in 1968 Wace found that it formed a hummocky meadow, with some individual plants assuming a pachycaul habit with 'trunks' to *c.* 50 cm high.

Tristan: *Bonomi* 1 (K, PRE, NBG [herb. Mus. Austro-Afric. 1117]), 5 (K, PRE, NBG [herb. Mus. Austro-Afric. 1119]); *Carmichael* s.n. (BM -holotype of *I. bicolor*), s.n. (BM -holotype of *I. squarrosa*), s.n. (BM); *Christophersen* 10 (O, K), 59 (O, K), 448 (O, K), 518 (O), 520 (O, K), 524 (O, K), 540 (O, K), 542 (O, K), 545a (O, K), 546 (O, K), 550c (O, K), 1204 (O, K), 1109 (O, K), 1111 (O, K), 1120 (O), 1266 (O, K), 1274 (O, K); *Dyer* 3543 (PRE, NBG, K), 3571 (PRE, NBG, K), 3571 bis (K); *Macgillivray* 341 (BM, K), 342 (K); *Mejland* 110 (O, K), 142 (O, K), 144 (O, K), 603 (O, K), 624 (O, K), 626 (O, K), 627 (O, K), 638 (O, K), 639 (O, K), 820 (O, K), 1141 (O, K), 1153 (O, K), 1117 (O, K), 1417 (O), 1424 (O), 1541 (O, K), 1650 (O); 1762 (O, K), 1764 (O, K); *Milne* s.n. (K); *Moseley* 6 (BM, K), 8 (BM, K -both syntypes of *S. prolifero-ramosus*), s.n. (K); *Siggeson* 50 & 51 (O)†; *Stableford* 93 (BM), 131 sterile (BM); *Thouars* s.n. (P -holotype of *S. prolifer); Wace* T.8 (BM), T.9 (BM), T.18 (BM), T.26 (BM), T.29 (BM), T.102 (K), T.116 (K), T.120 (K), T.226 (K), T.234 (K), T.249 (K), T.252 (K), T.259 (K). **Inaccessible:** *Christophersen* 2327 (O), 2392 (O, K), 2444 (O, K), 2474 (O, K), 2486 (O), 2519 (O, K), 2523 (O, K), 2524 (O, K), 2561 (O, K), 2585 (O, K); *Moseley* 8bis (BM, K -both syntypes of *S prolifero-ramosus: Wace* I.5 (K). **Nightingale:** *Christophersen* 2038 (O, K), 2043 (O, K), 2044 (O, K), 2094 (O, K), 2113 (O), 2169 (O, K), 2185 (O, K), 2235 (O, K); *Moseley* s.n. (K), 4 (K -holotype of *S. thouarsianus* var. *pallescens,* BM, E). **Gough:** *Brown* s.n. (K, E); *van der Merwe* 22 (PRE, K); *Wace* 16 (BM), 108 (BM), 121 (BM), G.216 (K), G.225 (K).

var. **virens** (Boeck.) Hemsley

S. virens Boeck.; *S. thouarsianus* var. *virens* (Boeck.) Hemsley; *S. oliveri* Boeck.

Endemic variety. First collected on Inaccessible Island by Moseley in 1873, and since found on all of the other islands. It occurs in moist situations similar to those of the typical variety and differs in its slender habit and by the distinct green apiculus of its glumes.

Tristan: *Bonomi* 2 (K, NBG [ex Herb. Mus. Austro-Afric. 1118]); *Christophersen* 57 (O, K), 1119 (O); *Dickson* 42 (BM, AAS), 93 (BM); *Dyer* 3571 (PRE, NBG, K), 3573 (PRE, NBG, BM, K); *Mejland* 1157 (O, K), 1163 (O, K). **Inaccessible:** *Christophersen* 2424 (O, K), 2437 (O, K), 2494 (O), 2588 (O, K), 2623 (O); *Moseley* s.n. (K -holotype of *S. virens,* BM), s.n. (K -holotype of *S. oliveri*). **Nightingale:** *Christophersen* 2002 (O, K), 2096 (O, K), 2114 (O, K), 2237 (O, K). **Middle:** *Christophersen* 2024 (O, K), 2025 (O, K). **Stoltenhoff:** *Christophersen* 2154 (O, K), 2155 (O, K), 2156 (O, K). **Gough:** *Brown* s.n. (K, E); *Wace* 18 (BM), G.233 (K), G.240 (K).

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*As has been pointed out by Hooper (1968: 5–6). *S. bicolor* exhibits a wide variation in size, growth form and glume coloration, as well as often occurring in a sterile or proliferous condition—a situation which has led to the description of a number of species and varieties all based upon small differences. In accordance with Hooper's treatment only the var. *virens* Boeck., in addition to that of the type variety, is maintained here.

† Not seen at O in 1973, but cited as being present by Christophersen (1937: 8–9).

Scirpus chlorostachyus Levyns

Isolepis subtilis Kunth; *Scirpus cernuus* var. *subtilis* (Kunth) C. B. Clarke

Possibly native. First collected on Tristan da Cunha by Macgillivray in November 1852 but not noted from any of the other islands in the group. This small, easily overlooked, species may be distinguished from both *Scirpus cernuus* and *S. verruculosus* (with which it is often in association) by its triangulate achenes. On Tristan it has been found in peat in boggy ground near Jenny's Watron, in wet hollows in grassland near the Settlement and at the Potato Patches, and in several other damp places.

Tristan: *Christophersen* 278 (O, K), 1326 (O, K); *Dickson* 44 (BM), 81 (BM); *Keytel* s.n. (NBG*); *Macgillivray* 340 (K), 340b (K), s.n. (BM); *Mejland* 143a (O, K), 177a (O, K), 605 (O, K), 1142 (O, K), 1159 (O, K); *Milne* s.n. (K), *Moseley* 3 (BM); *Siggesson* 49 (O†); *Wace* T.17 (BM), t.86 (BM), T.103 (K).

Scirpus sulcatus Thouars

var. **sulcatus**

Isolepis sulcata (Thouars) Carmich.

Endemic variety. First collected on Tristan da Cunha by Aubert Du Petit-Thouars in 1793, where it grows in damp and boggy situations or at the margins of pools, often associated with *Sphagnum*. In 1968 Wace collected specimens that were colonising new lava debris. The type variety is common on most of the main islands at altitudes from sea-level up to *c.* 670 m.

Tristan: *Carmichael* s.n. (BM); *Christophersen* 48 (O, K), 220 (O, K), 525 (O, K), 532 (O, K), 545b (O, K), 1023 (O, K), 1095 (O), 1107 (O, K), 1327 (O, K), 1328 (O, K); *Dickson* 29 (BM), 119 (BM), s.n. (BM); *Dyer* 3574 (PRE, NBG, BM, K); *Fleming* 71 (E); *Keytel* 1849 (K); *Macgillivray* s.n. (BM), 339 (K); *Mejland* 347 (O, K), 604 (O, K), 625 (O, K), 1110 (O, K), 1143, (O, K), 1144 (O), 1145 (O, K), 1146 (O, K), 1154 (O, K), 1169 (O, K), 1549 (O), 1576 (O), 1763 (O, K); *Milne* s.n. (K); *Moseley* 1 (BM), s.n. (K); *Stableford* 19 (K), 19c (K); *Thouars* s.n. (P -holotype); *Wace* T.19 (BM), T.38 (BM), T.81 (BM), T.100 (K), T.101 (K), T.222 (K), T.248 (K), T.260 (K). **Inaccessible:** *Christophersen* 2374 (O, K), 2396 (O), 2439 (O, K), 2443 (O, K), 2456 (O), 2457 (O), 2471 (O, K), 2499 (O, K), 2586 (O, K); *Dickson* 185 (BM); *Moseley* 2 (BM), s.n. (K); *Wace* I.21 (K). **Nightingale:** *Christophersen* 2036 (O, K), 2099 (O, K), 2100 (O, K), 2101 (O, K), 2102 (O, K), 2133 (O, K), 2134 (O); 2215 (O, K), 2223 (O, K); *Dickson* 136 (BM, AAS); *Wace* N.2 (K), N.4 (K). **Gough:** *Brown* s.n. (K); *Discovery 'W.S.' Exped.* s.n. (BM); *Wace* 17 (BM), 33 (BM), 82 (BM), 88 (BM), G.237 (K), G.247 (K), s.n. (K).

var. **moseleyanus** (Boeck.) Hemsley

S. moseleyanus Boeck.

Endemic variety. This is more slender than the typical variety, having a distinctly acuminate glume. Hemsley (1885: 155-6) reports with some reservation (as he had seen only a single specimen), that it is 'easily recognized by its deep red-brown leaf-sheaths'.

Tristan: *Macgillivray* s.n. (BM). **Inaccessible:** *Glass in Christophersen* 1286 (O, K); *Moseley* 9 (BM, E, K *pro parte*), s.n. (K), 2 (E). **Nightingale:** *Christophersen* 2039 (O, K), 2170 (O, K), 2171 (O, K), 2184 (O, K), 2222 (O, K), 2234 (O, K); *Dickson* 143 (BM); *Moseley* 7 (K -holotype, BM, E), s.n. (K); *Stableford* s.n. (K); *Wace* N.19b (K). **Gough:** *Brown* s.n. (K, E); *Discovery 'W.S.' Exped.* s.n. (BM); *van der Merwe* 22 (PRE—probably this variety); *Wace* 33a (BM), 88a (BM).

Scirpus verruculosus Steudel

Isolepis verruculosa (Steudel) Nees

Native. First collected on Tristan da Cunha in 1873 by Moseley during the *Challenger* Expedition but not re-found until the visit of the Norwegian Scientific Expedition in 1937. However it has probably been overlooked for it frequently occurs in association with *Scirpus chlorostachyus.*

Tristan: *Mejland* 130a (O, K), 130b (O), 143b (O, K), 602 (O); *Moseley* s.n. (K); *Wace* T.155 (K).

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*Not among sheets received (1975) on loan from NBG, but cited by Philips (1913: 99) as being collected from around the Settlement.

†Not seen at O in October 1973, but recorded by Christophersen as being there (Christophersen 1937: 8).

Uncinia brevicaulis Thouars var. **brevicaulis**

U. brevicaulis var. *gracilior* Hemsley; *U. brevicaulis* var. *rigida* (Boeck.) Kükenthal; *U. gracilis* Thouars, nom. illeg.

Native variety. First collected on Tristan by Aubert Du Petit-Thouars in 1793. Two varieties of *brevicaulis* have been described, the type variety being the taxon represented in the Tristan-Gough group and also on the islands of Amsterdam and St Paul, and the var. *macloviana* (Gaudich.) C. B. Clarke occurring on the Falkland Islands, Juan Fernandez and in Chile. The two varieties differ mainly in the shape of their bracts. In the former the bract is oblong and acute to acuminate and the utricle exceeds the glume in length, whilst in the latter the bracts are obtuse and the utricle is seldom longer than the glume. In the Tristan-Gough group var. *brevicaulis* is frequent in wet peat and bogs, and occasionally amongst damp grass in a mixed *Phylica/Blechnum* association.

Tristan: *Carmichael* s.n. (K, BM, O); *Christophersen* 453 (O, BM, K), 459 (O, BM, K), 1030 (O, BM). 1065a (O), 1094 (O), 1573 (O); *Dickson* 25 (BM, AAS); *Dyer* 3575 (PRE, NBG, K); *Macgillivray* 338 (K -holotype of *U. brevicaulis* var. *gracilior),* s.n. (BM); *Mejland* 824 (O, BM), 1179 (O, BM), 1358 (O), 1372 (O, BM), 1473 (O, BM, K), 1614 (O, BM); *Milne* s.n. (K); *Stableford* 2 (K); *Thouars* s.n. (P -holotype of *U. brevicaulis*); *Wace* T.37 (BM), T.221 (K). **Inaccessible:** *Christophersen* 2304 (O), 2390 (O, BM, K), 2473 (O, BM), 2563 (O, BM). **Nightingale:** *Christophersen* 2218 (O, BM, K); *Wace* N.32 (K). **Gough:** *van der Merwe* 54a (K); *Wace* 29 (BM), 58 (BM), 83 (BM), 136 (BM).

Uncinia compacta var. **elongata** C. B. Clarke

Native variety. First collected on Tristan da Cunha by Christophersen in December 1937. The typical variety occurs in Australia (New South Wales and Tasmania) whilst var. *elongata* is found only on the islands of the Tristan-Gough group and on Amsterdam and St Paul Islands. A summary of their differences is given by Hooper (1968: 7). In the Tristan-Gough group var. *elongata* grows in moss on bogs and also on damp cliffs, often in association with mats of *Empetrum.*

Tristan: *Christophersen* 43 (O, K), 64 (O, K), 516 (O, K), 1065 (O, K); *Dickson* 118 (BM, AAS); *Mejland* 633 (O, K), 1368 (O, K), 1371 (O, K), 1373 (O), 1379 (O, K), 1387 (O, K), 1517 (O, K), 1557 (O, K), 1614a (O), 1654 (O, K); *Wace* T.168 (K), T.228 (K). **Inaccessible:** *Christophersen* 2387 (O, K), 2470 (O), 2477 (O, K). **Gough:** *Wace* 24 (BM), 95 (BM), 113 (BM), 122 (BM), G232 (K -probably this species).

Uncinia meridensis Steyerm.

U. smithii Philcox

Native. First collected on Tristan da Cunha by Mejland in 1937. This small perennial sedge with a creeping rhizome and glaucous, crisp leaves, is frequent in bogs and wet heaths, particularly between 100–900 m where it often forms tufts or mats amongst *Rhacomitrium* moss and hepatics. In 1968 it was found also on Gough Island. See Hooper (1968: 7–8) for affinities; it is possible that *Uncinia sinclairei* from New Zealand is closely related.

Tristan: *Mejland* 1357 (O, K), 1615 (O, K); *Wace* T.214 (K), T.227 (K), T.229 (K). **Gough:** *Wace* G.231 (K).

GRAMINEAE

Agrostis carmichaelii J. A. Schultes & J. H. Schultes

Agrostis ramulosa Carmich. (1819), non. *A. ramulosa* (Kunth) Roemer & J. A. Schultes (1817).

Endemic. First collected on Tristan da Cunha by Carmichael in 1816 and described as *A. ramulosa* (Carmichael, 1819: 504). The species occurs in damp places.

Tristan: *Carmichael* s.n. (BM -holotype of *A. ramulosa*); *Christophersen* 47 (O, BM, K), 205, (O, K), 736 (O, K), 1265 (O, BM, K); *Macgillivray* 346 (K); *Mejland* 634 (O, BM, K), 637 (O, BM, K), 822 (O, K), 1382 (K), 1385 (K), 1562 (O, BM, K), 1590 (O, K), 1765 (O, K); *Wace* T.219 (K), T.318 (K -probably this species), T.348 (K). **Inaccessible:** *Christophersen* 2391 (O, BM, K), 2480 (O, K), 2505 (O, K). **Gough:** *Wace* 142 (BM), G.210 (K), G.249 (K).

Agrostis castellana var. **mixta** Hackel

Introduced. This grass is a loosely tufted perennial, with slender to somewhat stout rhizomes, stoloniferous, 30–70 cm high; culms slender to relatively stout; leaf-sheaths smooth; ligules of culm-leaves 1–3 mm long; blades up to 20 cm long and 2.5 mm wide. Panicles loose or finally contracted, variable in size, up to 16 cm long. Spikelets 2–3 mm long, those at the tips of the branches and branchlets awned, the lateral ones awnless; lemmas of terminate spikelets 3–5-nerved with the side-nerves minutely excurrent, sometimes pubescent on the sides, awned from just above the base, the awn geniculate, 1.5–3 mm long; basal callus minutely bearded; palea $\frac{1}{2}$ to $\frac{2}{3}$ the length of lemma; lemmas of lateral spikelets glabrous, 3-nerved, awnless.

It was first found for the group on Tristan da Cunha by Keytel during 1908–09. Since that time it has been collected on that island on a number of occasions, not only in pasture at the Settlement but also on the Peak slope, where it was observed as forming a dense sward on small ridges leading up a gully. It has also been collected once on Gough Island.

This grass may have been introduced from the Mediterranean region, or via South Africa, or some other part of the world where it has become established. It is often confused with *Agrostis tenuis.* The var. *mixta* is frequently found among the seeds of the turf-forming grass 'Highland Bent', which are exported from the United States. This and other varieties of *A. castellana* hybridise with *A. tenuis* yielding a wide range of intermediates.

Tristan: *Christophersen* 300a (O), 402a (O); *Dyer* 3534 pro parte (PRE, BM, K), 3551 (O, K, PRE, NBG); *Keytel* 1838 (K); *Mejland* 173 (O, BM). *Stableford* 7 pro parte. **Gough:** *van der Merwe* 71 pro parte (PRE, K).

Agrostis crinum-ursi Mez

Endemic (?). A grass from Tristan da Cunha gathered by an unknown collector (prior to 1921) and deposited in the Berlin herbarium, was described by Carl Mez (*Reprium Spec. nov. Regni veg.* **17:** 300 (1921)) under the above name. In his description Mez gave it as being a densely caespitose perennial, up to 17 cm high, with finely filiform-subulate rather rigid leaf-blades, up to 4 cm long, few spiculate inflorescences 2.5 cm long by 5 mm wide, and spikelets up to 2.2 mm long, with awnless 5-nerved lemmas. It may be one of the imperfectly known tufted species since gathered at the islands, but unfortunately the type material was destroyed in 1943.

Agrostis gigantea Roth

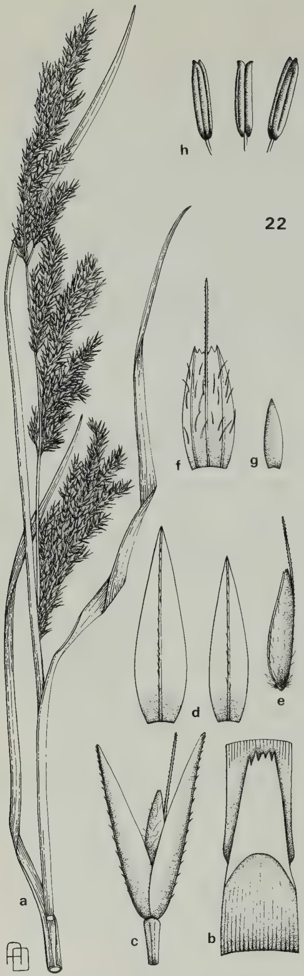
Introduced. This species was first collected on Tristan da Cunha by Mejland during the Norwegian Scientific Expedition of 1937–38. It was found growing near the Settlement. *A. gigantea* has been gathered again there since and also on Inaccessible Island, near a ruined cottage at Saltbeach.

Tristan: *Dickson* 97 (K); *Mejland* 2199 (O, K). **Inaccessible:** *Dickson* 130 (K).

Agrostis goughensis C. E. Hubbard, **sp. nov.** (Fig. 22)

a *A. stoloniferae* spiculis longioribus, lemmatibus pubescentibus aristatis, callis dense barbatis differt.

Perennial, forming mats. Culms up to 80 cm long, ascending from a creeping base, rooting at the nodes, stoloniferous, up to 7-noded, comparatively stout, terete, glabrous, smooth. Leaf; sheaths finally shorter than the internodes, glabrous, smooth; ligules oblong, obtuse, membranous, up to 10 mm long; blades narrowly linear, tapering to an acute tip, flat, up to 25 cm long and to 6 mm wide, finely ribbed above, scaberulous on the ribs and margins, smooth beneath, green. Panicles oblong, inclined, rather congested, up to 23 cm long and to 3 cm wide; rhachis scabrid; branches densely clustered, unequal, spreading, up to 5 cm long, divided, with filiform scaberulous, closely spiculate branches and branchlets; pedicels 1–4 mm long, scaberulous. Spikelets 4–4.5 mm long, lanceolate, acute, narrowly oblong-lanceolate when opened out, keeled, scaberulous on the keel, membranous, 1-nerved, the lower as long as the spikelet, the upper narrower than the lower and slightly shorter; lemma 2–2.3 mm long, ovate-oblong when opened out, obtuse, hyaline, finely 5-nerved, finely and appressedly thinly pubescent, awned from the upper third of the lemma; awn straight, minutely scaberulous, fine, up to 2.5 mm long; callus densely bearded with white hairs up to 0.5 mm long. Palea ovate-oblong, obtuse, 1 mm long, hyaline finely 2-nerved. Anthers 0.8–1 mm long.



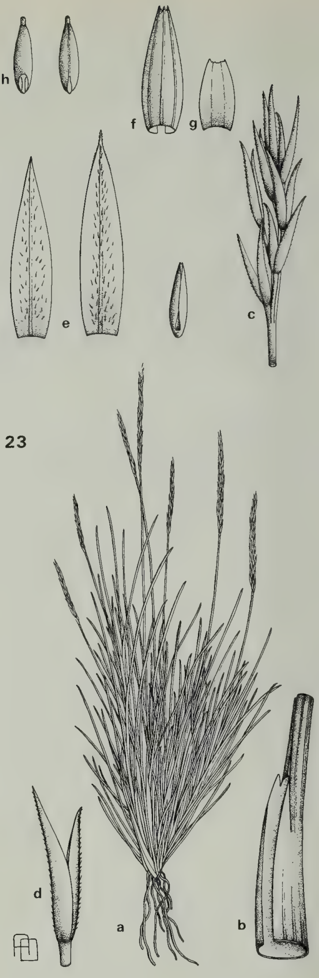


Fig. 22 *Agrostis goughensis* C. E. Hubbard. a. habit (x $\frac{1}{2}$); b. ligule (x 3); c. spikelet (x 10); d. glumes (x 10); e. floret (x 10); f. lemma (x 10); g. palea (x 10); h. stamens and ovary (x 13). All drawn from *Wace* 49.

Fig. 23 *Agrostis holgateana* C. E. Hubbard. a. habit (x $\frac{2}{3}$); b. ligule (x 7); c. raceme (x 3); d. spikelet (x 7); e. glumes (x 8); f. lemma (x 8); g. palea (x 8); h. grain (x 7). Drawn from *Wace* T. 235.

Endemic. First found for the group on Gough Island in December 1955 by Wace, who discovered it forming mats with stolons over freshwater pools and around wet places. It has the same stoloniferous habit and similar long ligules to that of *A. stolonifera* L. subsp. *stolonifera,* but its spikelets are larger and have thinly pubescent awned lemmas, and a minutely bearded callus.

Gough: *Wace* 49 (BM -holotype).

Agrostis holgateana C. E Hubbard, **sp. nov.** (Fig. 23)

a *A. mediae* Carmich., habitu dense caespitoso, culmis rigidis, laminis setaceis, paniculis linearibus vel lanceolato-linearibus densis, spiculis longioribus differt.

Perennial, densely caespitose, 9–28 cm high; innovations intravaginal. Culms erect or slightly spreading, stiff, filiform, branched and several-noded in the lower part, leafy, glabrous, smooth, the uppermost internode exserted. Leaf-sheaths overlapping, glabrous, smooth, glossy; ligules ovate-oblong to oblong, obtuse or truncate, 1–2.5 mm long, firmly membranous to chartaceous; blades setaceous, obtuse to subacute, stiff, erect, tightly involute, straight or slightly curved, 3–6 cm long, 0.4 - 0.6 mm in diameter, scaberulous on the margins. Panicle linear to lanceolate-linear, spike-like, erect, 1.5–3.5 cm long, up to 4 mm wide, dense; rhachis smooth; branches unequal, erect, 2–3-nate, up to 15 mm long; pedicels 0.5–2.5 mm long. Spikelets 4–5 mm long, narrowly oblong, sharply acute, appressed to the branches; glumes unequal, sharply acute, keeled, prominently scabrid on the keel and on the surfaces, narrowly lanceolate in profile, narrowly oblong-lanceolate when opened out, coriaceous, the lower as long as the spikelet, with the tip slightly recurved, 1-nerved, the upper 0.5–1.5 mm shorter than the lower, also narrower, finely 3-nerved. Lemma ovate-elliptic when opened out, 1.6–1.7 mm long, minutely 2-lobed, or truncate and minutely denticulate, 3–5-nerved, with the middle nerve ending in a mucro or a short straight awn up to 0.8 mm long, smooth, membranous: callus minute, glabrous. Palea about two-thirds the length of the lemma, oblong, truncate-emarginate, membranous, finely 2-nerved, smooth. Grain 1–1.2 mm long, lanceolate to oblong in outline.

Endemic. First collected for the group on Tristan da Cunha in 1968 by Wace who found it at three localities: to the north and east of Round Hill (including Soggy Plain), beside a small tarn in the crater of Green Hill, and at the base of Tristan Peak at 1060 m. At each of these sites the grass was found growing in damp conditions associated with sedges and mosses including *Sphagnum. Agrostis holgateana* is distinguished from other Tristan species of *Agrostis* by its stiff dense form of growth, its very slender rigid culms and leaf blades, and its erect spike-like panicles. It has been named in honour of Dr Martin W. Holgate, leader of the 1955 Gough Island Scientific Survey Expedition.

Tristan: *Wace* T.177 (K), T.218 (K), T.206 (K), T.235 (K -holotype).

Agrostis lachnantha Nees

Introduced. First collected in 1957 by van der Merwe and then by Wace in 1968. Both collectors found it growing by paths and on disturbed ground near the Meteorological Station.

Gough: *van der Merwe* 62 (PRE, K); *Wace* G.251 (K).

Agrostis magellanica subsp. **laeviuscula** C. E. Hubbard, **subsp. nov.**

a subsp. *magellanicae,* rhachidi et ramis et ramulus et pedicellis laevibus, glumarum carinis breviter scabridis vel fere laevibus, aristis brevioribus strictis, paleis minoribus differt.

Perennial, stoloniferous or tufted, 10–30 cm high; stolons wiry. Culms tufted or ascending from a many-noded trailing base, slender, several-to-many-noded, closely branched or simple, closely sheathed, glabrous, smooth. Leaf-sheaths striate, longer than the internodes, glabrous, smooth; ligules oblong, very obtuse, thinly membranous, 1.5–6 mm long, becoming lacerate; blades linear, pungent-acute or obtuse, 2–16 cm long, 1–4 mm wide, flat, firm, green, closely and prominently ribbed above, with the ribs minutely hispid or scabrid, smooth and glabrous beneath. Panicles lanceolate to narrowly oblong, contracted and rather dense to somewhat lax, or slightly lobed, green, 4–16 cm long, 1.5–3 cm wide; rhachis smooth, glabrous; branches fascicled, divided, smooth, glabrous; pedicels thickened towards their tips, 2–4 mm long, smooth. Spikelets up to 5.5 mm long, narrowly lanceolate to narrowly oblong, or finally gaping. Glumes very finely acute, shortly aristate-acuminate, straight or with the tips slightly recurved, keeled, glabrous, slightly scabrid on the keels, otherwise smooth, 1-nerved, firmly membranous except for the thinner margins; lower lanceolate opened out, 4.5–5.5 mm long; upper from four-fifths to almost as long as the lower, narrowly lanceolate opened out. Lemma ovate-elliptic or elliptic, 1.7–1.8 mm long, slightly and obtusely lobed or truncate, thinly membranous, very minutely and obscurely verrucose, glabrous, finely 5-nerved, with the lateral nerves sometimes minutely excurrent, awned from the back towards the tip, with the awn fine, straight, up to 2.5 mm long, minutely scaberulous; palea 0.8–1 mm long, oblong, obtuse; rhachilla not produced; callus glabrous. Anthers 0.8 –1 mm long. Grain, oblong, dorsally compressed, 1.5 mm long.

Agrostis magellanica Lam. (*Tabl. Encycl.* **1:** 160 (1791)) was based on plants collected by Commerson in the eastern Magellan; it is widespread in the south Antarctic, and differs in the ramifications of the panicle being minutely hispidulous, the equal or subequal similar glumes scabridly-hispidulous on the keels, and the awns geniculate.

Endemic subspecies. It was first found both on Tristan da Cunha and on Inaccessible Island early in 1938, during the Norwegian Scientific Expedition visit to the group. On Tristan it occurs in grassy areas just above the tree-fern limit. It has more recently been collected on Gough Island.

Tristan: *Christophersen* 1584 (K); *Mejland* 1364 (O, K, BM), 1551 (K -holotype, O, BM), 1564 (K); *Wace* T.166 (K), T.173 (K), T.173 (K), T.233 (K). **Inaccessible:** *Christophersen* 2521 (O, K, BM). **Gough:** *Wace* G.236 (K), G.246 (K).

Agrostis media Carmich.

Endemic. First collected on Tristan da Cunha by Carmichael in 1816-17, who described his material as a new species. It occurs frequently over the island on grassy slopes amongst the tree-fern scrub between 600 and 800 m, and has also been found on Inaccessible and Gough Islands.

Tristan: *Carmichael* s.n. (BM -holotype); *Christophersen* 50 (O, K, BM), 61 (O, K), 211 (O, K), 523 (O, K, BM), 549b (O, K), 550f (O, K, BM), 550g (O, K, BM), 1325 (O, K); *Dickson* 33 (K); *Mejland* 1366 (O, K, BM), 1367 (O, K), 1381 (O, K, BM), 1382 (O, K, BM), 1384 (O, K, BM), 1385 (O, K, BM), 1574 (O, K); *Milne* s.n. (K); *Moseley* s.n. (K); *Wace* T.196 (K), T.225 (K), T.318 (K). **Inaccessible:** *Christophersen* 2472 (O, K), 2508 (O, K). **Gough:** *Brown* s.n. (K); *Fleming* 25 (E); *van der Merwe* 67b (PRE); *Wace* 72 (BM), 74 (BM), 91 (BM), 123 (BM), G211 (K), G.248 (K), G.249 (K).

Agrostis stolonifera L. subsp. **stolonifera**

A prostrata J. D. Hook.; *A. difficilis* Hemsley

Introduced. First collected on Tristan da Cunha by Mejland in January 1938. It has now become a common weed on the Settlement Plain and at the Potato Patches, where it is quick to spread on disturbed ground. It has also been found on both Inaccessible and Gough Islands, where on the former it is now frequent at the foot of the cliffs and around the huts at Waterfall Beach, and on the latter it has been found forming mats among native grasses and sedges.

Tristan: *Christophersen* 296 (O, K, BM); *Dickson* 91 (K); *Mejland* 1166 (O, BM, K), 1309 (O, BM, K); *Stableford* 36 (sterile) (BM), 49 (BM); *Wace* T.80 (BM), T.255a(2) (K). **Inaccessible:** *Wace* I.23 (K), I.50 (K); **Gough:** *van der Merwe* 71 pro parte (K); *Wace* 48 (BM), 130 (BM), 134 (BM), G.250 (K).

Agrostis tenuis Sibth.

A. simulans Hemsley

Introduced. First collected on Gough Island when the RRS *Discovery* II called there in June 1927 on her homeward voyage after a season of Antarctic surveys. It has also been found on several occasions on Tristan da Cunha occurring as a common grass in pastures near the Settlement and at the Potato Patches. More recently it was discovered forming a deep sward on slopes below the cliffs behind the new volcano.

Tristan: *Christophersen* 270a (O), 271 (O), 300 (O), 402 (O), 1131 (O, BM, K), 1331 (O, BM); *Dickson* 22 (BM), 53 (BM), 90 (BM), 173 (BM—probably this species); *Dyer* 3534 pro parte (K, BM);

Mejland 173 (O, BM); *Stableford* 6 (K); 7 pro parte (K), 48 (BM), 109 (BM); *Wace* T.108 (K), T.123, (K), T.130 (K), T.255a (1) (K). **Gough:** *Discovery 'W.S' Exped.*, s.n. (BM); *van der Merwe* 71 pro parte (PRE); *Wace* 47 (BM).

Agrostis trachychlaena C. E. Hubbard, **sp. nov.** (Fig. 24)

a. *A. stoloniferae* L., foliorum lamina supra scabra vel minute hispida et prominenter et arcte striata, glumis hispido-scabris demum deciduis differt.

Perennial, loosely tufted. Culms trailing, probably stoloniferous, ascending from a creeping base, 20–55 cm long slender, many-noded, profusely branched, glabrous, smooth. Leaf-sheaths overlapping, terete, persistent, prominently striate, the ribs minutely scaberulous or smooth, glabrous; ligules oblong, 1–3 mm long, thinly membranous, becoming lacerate; blades linear, finely acute, 2–7 cm long, 0.5–2 mm wide, flat, spreading, prominently and closely ribbed on the upper surface, with the ribs scabrid or minutely hispid, glabrous and smooth beneath. Panicles shortly exserted from the uppermost sheaths, narrowly lanceolate to narrowly oblong, contracted and rather dense, 1.5–5.5 cm long, 6–16 mm wide; rhachis smooth or slightly hispid; branches 3–5-nate, slightly flexuous, stiff, erect or spreading obliquely, divided, 0.3–1.5 cm long, scabro-hispid; pedicles thickened upwards, club-shaped, 0.3–2 mm long, scabro-hispid, sometimes apparently articulated at the base. Spikelets linear to linear-lanceolate, acute, 3–4 mm long. Glumes acute, conspicuously hispidly scabrid, firmly membranous, finally deciduous; lower as long as the spikelet, lanceolate opened out, 1–3-nerved; upper three-fourths to four-fifths the length of the lower, lanceolate opened out, 1–3-nerved. Floret slightly dorsally compressed; rhachilla not produced; lemma 1.3–1.8 mm long, ovate-oblong, broadly very obtuse or dentate-truncate, thinly membranous, 5-nerved, with the nerves reaching the tip or minutely excurrent; palea broadly oblong, very obtuse, minutely scaberulous, 2-nerved, smooth, 0.6–0.8 mm long. Grain immature, triquetrous, narrowly oblong, 1 mm long.

Endemic. First discovered for the group by Christophersen on both Inaccessible and Nightingale Islands, in early 1938, during the Norwegian Scientific Expedition. Found on damp rocks or on rocky slopes in the shade of tussock *(Spartina arundinacea)* where sheltered and in damp conditions. Not yet recorded from any of the other islands. It is a most distinct species, unlike any other *Agrostis* from South Africa, tropical Africa, the Mascarenes or Atlantic Islands.

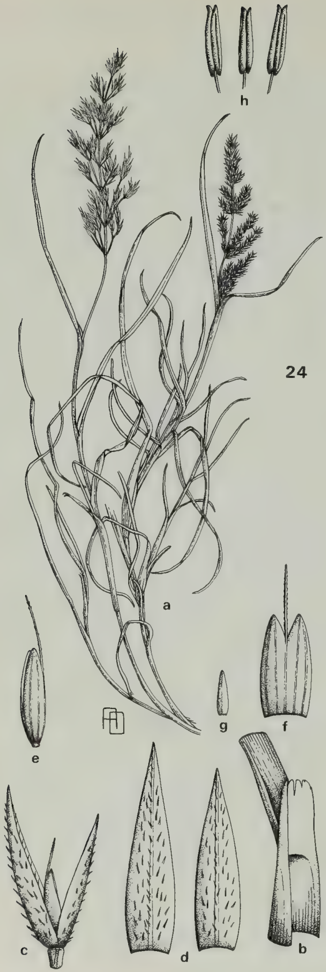
Inaccessible: *Christophersen* 2578 (K -holotype, O). **Nightingale:** *Christophersen* 2213 (O, BM, K); *Wace* N.6 (K), N.33 (K), N.51 (K).

[Agrostis tropica Beauv.

Palisot de Beauvois (1813, II, 37 T.80, fig, 2) described this species from a specimen collected by Aubert Du Petit-Thouars from Ile de Prince (Principé) and said that the same collector also found it in Mauritius. Not only is the type of the grass no longer available for study (although Beauvois' illustration is good) but subsequent collectors have failed to rediscover it on either island. This is perhaps understandable as neither has a suitable habitat. Aubert Du Petit-Thouars was, however, also known to have visited the islands of Tristan da Cunha and réunion (see p. 347) during the same voyage and that some of his specimens, labelled subsequent to collection, became wrongly localised (see note under *Amauropelta bergiana*, p. 404). It is possible, therefore, that the specimen on which Beauvois' *Agrostis tropica* was based came not from Principé, but from Tristan da Cunha or Réunion. No specimen of any *Agrostis* from Tristan da Cunha seen so far matches Beauvois' illustration of *A. tropica* (=pubescent glumes, cf. scabrid or glabrous glumes of all the Tristan da Cunha *Agrostis*), and while the possibility of finding it on that island cannot entirely be ruled out, it would seem that Réunion is the more likely locality for this grass.]

Agrostis wacei C. E. Hubbard, **sp. nov.** (Fig. 25)

gramen perenne compacte caespitosum glaucum; culmi tenuiter filiformes, flexuosi, multinodes, ramosi, laeves; laminae numerosae, tenuiter filiformes, obtusae, breves, teretes, involutae, glabrae; ligulae brevissimae; racemi 1–4-spiculati, breves; spiculae oblongae, 1.6–2 mm longae; glumae aequales vel paullo inaequales, minute scabridae; lemma truncatum, minute 5-dentatum, glabrum, 5-nerve; palea fere lemmate aequilonga.



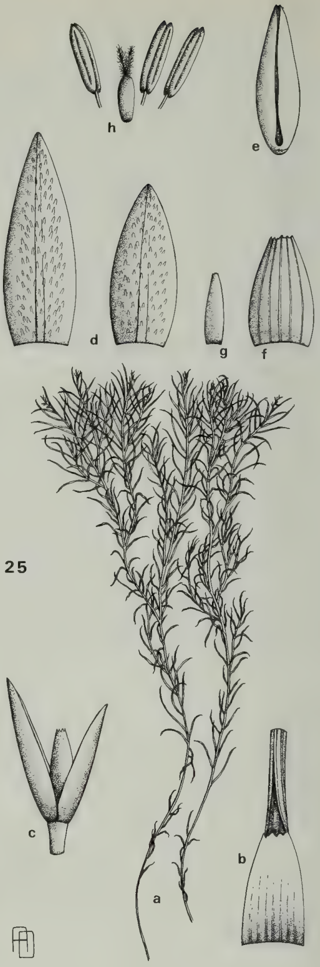


Fig. 24 *Agrostis trachychlaena* C. E. Hubbard. a. habit (x ⅔); b. ligule (x 4); c. spikelet (x 10); d. glumes (x 13); e. floret (x 13); f. lemma (x 13); g. palea (x 13); h. stamens (x 13). The habit and ligule are drawn from *Christophersen* 2578; the remainder are drawn from *Wace* N. 51.

Fig. 25 *Agrostic wacei* C. E. Hubbard. a. habit (x ⅔); b. ligule (x 13); c. spikelet (x 13); d. glumes (x 20); e. floret (x 27); f. lemma (x 20); g. palea (x 20); h. stamens and ovary (x 15). All drawn from *Wace* T. 319.

Densely caespitose, forming soft hummocks up to 20 cm or more in diameter, up to 12 cm high. Culms finely filiform, terete, flexuous, many-noded, branched, leafy, glabrous, smooth. Leaves very numerous, glaucous when fresh (ex Wace); sheaths overlapping, longer than the internodes, finely ribbed, thin, glabrous, very minutely scaberulous; ligules ovate-oblong or oblong, up to 1 mm long, membranous; blades finely filiform, obtuse spreading obliquely, 10–14 mm long, terete, involute, glabrous, very minutely and obscurely appressed scaberulous, rather stiff, curved or straight. Inflorescence a raceme, 1–4-spiculate, 3–7 cm long, shorter than the terminal leaves; rhachis straight or slightly flexuous; pedicels up to 1.5 mm long. Spikelets oblong or gaping, 1.6–2 mm long. Glumes equal or unequal with the lower longer and as long as the spikelet, oblong to lanceolate-oblong, obtuse or acute, keeled, minutely scabrid all over, rigid on the keel, otherwise membranous, 3-nerved; lemma 1.2–1.4 mm long, broadly elliptic, truncate, minutely 5-dentate, awnless, thinly to firmly membranous, glabrous, smooth, 5-nerved; cellus very obtuse, glabrous; palea oblong, 1 mm long, glabrous, hyaline; anthers 1 mm long.

Named in honour of Dr Nigel M. Wace, botanist on the 1955 Gough Island Scientific Survey Expedition. His collections have added measurably to our knowledge of the flora of the group.

Endemic. First discovered for the group on Tristan da Cunha in November 1976 by Wace who found it growing amongst clumps of *Blechnum palmiforme* on the precipices under Big Green Hill at *c.*500 m alt., and forming soft hummocks up to 20 cm or more in diameter and very glaucous when fresh. *Agrostis wacei* is a very distinct grass, apparently not closely related to any of the other Tristan or African species of *Agrostis.*

Tristan: *Wace* T.319 (K -holotype, BM).

Three other examples of *Agrostis* collected by Wace (T.195, T.223 and T.224) also from Tristan da Cunha, represent a species allied to *A. wacei* but distinguished by their slightly larger, smooth glumes up to 3 mm long (cf. glumes in *A. wacei* up to 2 mm long). The material collected under all the above three numbers, however, is unfortunately either sterile or inadequate for description. Further collection of this *Agrostis* is therefore desirable.

Agrostis sp.

Phalaris cespitosa Thouars (1808: 37)

Endemic (?). Amongst the grasses found by Aubert Du Petit-Thouars on Tristan in 1793 was one which he regarded as new and gave the following short description (Aubert Du Petit-Thouars, 1808: 37, 84), 'Panicula pauciflora subspicata culmo repente stolonifero. Herb, I^{re}. Petite espèce à chaume rampant stolonifère; panicule pauciflore, resseré en un épi long d'un pouce. Cette plants couvre quelque fois, à elle seule, un grand espace de terrain.' Judging from this brief account, the grass is probably a species of *Agrostis* with stolons and spreading culms and with few flowered, spike-like panicles 2.5 cm long.

Tristan: *Thouars* s.n. (P*).

Aira caryophyllea L.

Introduced. First collected on Tristan da Cunha in 1937 and on Inaccessible Island in 1938, both during the visit of the Norwegian Scientific Expedition. On Tristan da Cunha it has been found in pasture grassland around the Settlement, where it has become frequent, and also along track sides or as a coloniser of bare patches. On Inaccessible Island it has been found growing on the steep slopes above Blenden Hall.

Tristan: *Christophersen* 2 (O, K), 109 (O); *Dickson* 8 bis (K), 16 (BM); *Mejland* 109 (O); *Stableford* 88 (BM), 117 (BM); *Wace* T.87 (BM), T.105 (K), T.132 (K), T.231 (K), T.311 (K), T.312 (depauperate) (K). **Inaccessible:** *Christophersen* 2481 (O, BM), 2487a (O).

Anthoxanthum odoratum L.

Introduced. First collected on Tristan da Cunha by Siggeson in November 1934. It occurs quite commonly in pasture at the Settlement and at the Potato Patches.

Tristan: *Christophersen* 272 (O, BM, K); *Mejland* 161 (O); *Siggeson* 55 (O); *Stableford* 12 (K), 12a (K), 37 (BM), 86 (BM); *Wace* T.48 (BM).

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* It was not possible to find the holotype on my visit there in September 1975.

Bromus willdenowii Kunth

B. catharticus auct., non Vahl; *B. unioloides* auct., non (Willd.) Kunth

Introduced. First collected on Tristan da Cunha in 1852 by Macgillivray and also by Milne, both on the voyage of HMS *Herald.* It occurs on that island by the edges of paths and on ungrazed pasture near the Settlement. More recently, in 1968, it has been found growing in sand against the new lava blocks at the level of the old sea beach.

Tristan: *Dickson* 50 (BM); *Macgillivray* 347 (K), s.n. (K); *Milne* s.n. (K); *Stableford* 2 (K), 41 (BM); *Wace* T.49 (BM), T.152 (K), T.261 (K).

Calamagrostis deschampsiiformis C. E. Hubbard, **sp. nov.** (Fig. 26)

gramen perenne dense caespitosum, 35–50 cm altum; culmi erecti, simplices, 2-nodes; foliorum vaginae laeves, basales persistentes, coriaceae; ligulae acutae, 3–7 mm longae; laminae junciformes, obtusae, cylindricae, involutae, rigidae, 8–19 cm longae, 1–1.2 mm latae, glabrae; paniculae oblongae 13 cm longae; rami fasciculatae; pedicelli 1–4 mm longi; spiculae 8–10 mm longae; glumae explanatae anguste oblongae vel oblongae, acutae; inferior 1-nervis, superior 3–5-nervis; lemma 4.5–5 mm longum, bilobum, lobis plerumque acute bidentatis, aristatum, chartaceum, 7-nerve, laeve; ariste leviter geniculata vel flexuosa, 5.5–8 mm longa; callus pilis 1–1.6 mm longis barbatus; palaea oblonga, 4.5–5 mm longa, bicarinata, carinis scaberulis; caryopsis 2 mm longa.

A densely caespitose leafy perennial, 35–50 cm high, with numerous intravaginal innovations. Culms erect, stiff, moderately slender, 2-noded, simple, glabrous, smooth. Leaf sheaths glabrous, smooth; basal sheaths persistent, coriaceous, up to 8 cm long; ligules narrowly ovate, acute, 3–7 mm long, firmly membranous; blades junciform, erect, rigid, with coriaceous obtuse tips, cylindrical, involute, 8–19 cm long, 1–1.2 mm in diameter, smooth, closely ribbed and glabrous above. Panicles oblong, 13 cm long, 2–3 cm wide, loose; rhachis smooth below, sparsely scabrid above; branches clustered, up to 9 cm long, more or less scabrid; pedicels 1–4 mm long. Spikelets oblong or gaping, 8–10 mm long; rhachilla produced as a plumrose bristle up to 3 mm long, sometimes bearing an awn up to 3 mm long on a minute vestige. Glumes, slightly unequal, the upper as long as the spikelet, chartaceous-membranous, glabrous, smooth or the lower scabrid on the keel; lower linear-lanceolate in profile, acute, narrowly oblong when opened out, 7–9 mm long, keeled, 1-nerved; upper oblong when opened out, acute, 3–5-nerved. Lemma oblong when opened out, 4.5–5 mm long, 2-lobed with the lobes acutely and unequally 2-toothed, or acutely 5-toothed at the apex, firmly membranous-chartaceous to stiffly chartaceous, rounded on the back, 7-nerved, smooth, awned on the back in the lowest third; callus truncate, bearded with hairs 1–1.6 mm long, awn slightly geniculate or flexuous, 5.5–8 mm long, scaberulous; palea oblong, 2-toothed, as long as the lemma, 2-keeled with the keels scaberulous, firmly membranous. Caryopsis 2 mm long, oblong in side view, rounded on both sides, dark brown; embryo broadly elliptic; hilum oblong.

Endemic. First found by Wace on Tristan da Cunha in April 1968 and then on Gough Island in the following month. On Tristan it grew in the wet peaty margin amongst mosses beside Crater Lake on Stony Beach Hill, and on Gough in wet heath vegetation in Gonydale beside streams and wet gullies.

Tristan: *Wace* T.251 pro parte (K). **Gough:** *Wace* G.219 (K -holotype).

The species of *Calamagrostis* (sensu lato) are much in need of critical investigation. They appear to have had several different lines of evolution, some having *Deschampsia, Trisetum,* or other ancestral genera. The above new species belongs to a group well represented in parts of the Southern Hemisphere (South America, New Zealand and southern Australia), sometimes separated under *Deyeuxia,* in which the lemma is finally indurated and chartaceous to coriaceous. Until the complex has been studied in greater detail, it seems best to treat them in the broad sense, e.g. under *Calamagrostis.* This new species may have originated from a species of *Deschampsia,* such as *D. christophersonii,* in which a mixture of 2- and 1-flowered spikelets may be found, sometimes in the same inflorescence.

Cynodon dactylon (L.) Pers.

Introduced. First collected on Tristan da Cunha by Dyer in February 1937 and since found several times on the island in pasture by the Settlement and above high water on the beach.

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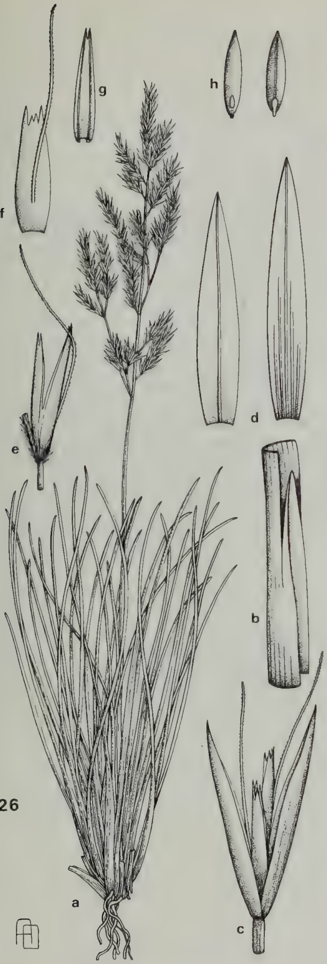

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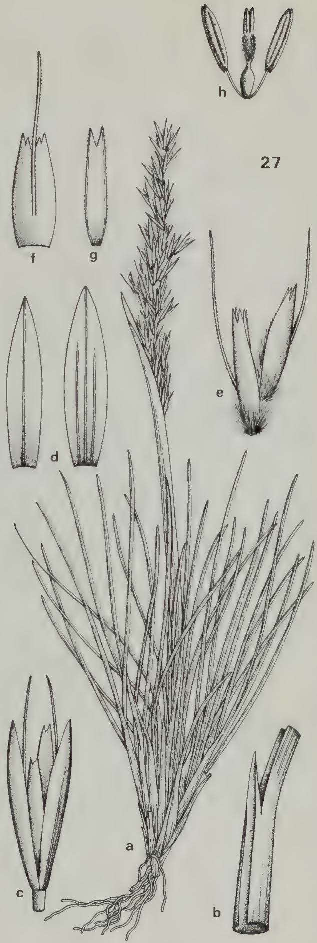

Fig. 26 *Calamagrostis deschampsiiformis* C. E. Hubbard. a. habit (x ½); b. ligule (x 4); c. spikelet (x 4); d. glumes (x 5); e. floret (x 5); f. lemma (x 5); g. palea (x 5); h. grain (x 8). The habit and ligule are drawn from *Wace* T. 251; the remainder are drawn from *Wace* G. 219.

Fig. 27 *Deschampsia christophersenii* C. E. Hubbard. a. habit (x ⅔); b. ligule (x 3); c. spikelet (x 4); d. glumes (x 4); e. florets (x 4); f. lemma (x 4); g. palea (x 4); h. stamens and ovary (x 8). All drawn from *Christophersen* 551.

More recently a single patch was found near the huts at Waterfall Beach on Inaccessible Island by Wace in February 1968.

Tristan: *Christophersen* 15 (O); *Dickson* 4 (BM), 146 (BM, K); *Dyer* 3540 (PRE, K, BM, NBG, O); *Mejland* (O, BM, K), 1297 (O, BM); *Stableford* 9 (K), 40 (BM), 91 (BM), 92 (BM), 114 (BM); *Wace* T.190 (K), T.327 (K), T.342 (K). **Inaccessible:** *Wace* I.16 (K).

Cynosurus cristatus L.
Introduced. Collected on Tristan da Cunha during 1953–54. It was probably originally imported in a mixed pasture seed.

Tristan: *Stableford* 15 (K), 34 (BM).

Dactylis glomerata L.
Introduced. First collected on Tristan da Cunha in 1954 by Stableford, who considered it to have been introduced in 1953 from South Africa. Wace in December 1955 found two clumps growing on Gough Island, above Glen Beach. He too considered it to be 'apparently recently introduced'.

Tristan: *Stableford* 8 (K), 44 (BM); *Wace* T. 187 (K). **Gough:** *van der Merwe* 72 (K); *Wace* 45 (BM).

Deschampsia christophersenii C. E. Hubbard, **sp. nov.** (Fig. 27)
a *D. mildbraedii* Pilger, ligulis brevioribus, foliorum laminis plerumque laevibus, paniculis angustioribus anguste oblongis vel lanceolato-oblongis, lemmatibus tenuioribus, callorum pilis longioribus differt.

Densely tufted perennial, 15–40 cm high, with many intravaginal innovations. Culms erect, simple, moderately slender, stiff, 2-noded closely sheathed. Leaf-sheaths overlapping, glabrous, smooth, the lower coriaceous, persistent, up to 7 cm long; ligules lanceolate, acute, 2–5 mm long, firmly membranous; blades erect, rigid, setaceously junciform, with the hard pungent or obtuse tip, convolute or complicate-involute, 5–20 cm long, 0.8–1.2 mm wide, smooth beneath, closely and prominently ribbed above, with the ribs glabrous and smooth, 2–2.5 mm wide opened out. Panicles dense to rather loose, erect, narrowly oblong to lanceolate-oblong, 7–15 cm long, 1–2 cm wide, greenish-yellow; rhachis glabrous towards the base, otherwise minutely hispid; branches slender, erect or ascending, up to 6 cm long, minutely hispid or glabrescent; pedicels 0.5–4 mm long, glabrous or slightly hispid. Spikelets narrowly oblong or gaping, 2-flowered; rhachilla ciliate, continued as a plumose bristle beyond second floret and sometimes tipped with a vestige. Glumes similar, equal or nearly so or lower slightly longer than upper, chartaceous except for the membranous margins, scaberulous on keel above the middle; lower 7.5–10 mm long, narrowly oblong-lanceolate to narrowly elliptic opened out, acute, 1–3-nerved; upper 7.5–9 mm long, narrowly elliptic or oblong-elliptic opened out, acute, 3-nerved, with the lateral nerves extending to the middle. Lower lemma ovate-oblong, 2-lobed, with the lobes unequally and acutely 2-toothed, 4.5–6 mm long, firmly membranous or coriaceous and smooth below, thinly to firmly membraneous and smooth or minutely scaberulous above the middle, 5–7-nerved, awned; awn slightly geniculate, 6–8 mm long, minutely scaberulous, arising in the lowest third of the lemma; callus densely bearded with white hairs 2–2.5 mm long; palea nearly as long as the lemma, narrowly oblong, acutely 2-toothed, minutely ciliate on the keels, thinly membranous; anthers 1–1.5 mm long. Upper lemma 4–5 mm long, ovate-oblong unequally acutely 4-toothed, 5–7-nerved, membranous to coriaceous, otherwise similar to the lower; awn 4–6.5 mm long; palea similar to that of lower floret; anthers 1–1.7 mm long.

Endemic. First found for the group on Tristan da Cunha and Inaccessible Island early in 1938, during the visit to the islands by the Norwegian Scientific Expedition, the several collections being made mostly in damp meadows or bogs between 600–900 m. It was again found on Tristan da Cunha in February 1962 by Dickson just above Hottentot Gulch and not far from the locality of *Mejland* 1383 (see below). This grass has been named in honour of Dr Erling Christophersen, leader and botanist on the Norwegian Scientific Expedition 1937–38. The botanical and other scientific results of this expedition made an outstanding contribution to our knowledge of the Tristan da Cunha group of islands.

Tristan: *Christophersen* 551 (O, K -holotype), 1105 (O, K); *Dickson* 120a (K); *Mejland* 1383 (O, K), 1556 (O, K); *Wace* T.76 (possibly this species but material sterile) (BM). **Inaccessible:** *Christophersen* 2469 (O, K).

In addition to the holotype of *Deschampsia christophersenii* cited above, in which the spikelets so far as they have been examined appear to be all 2-flowered, there are other specimens which closely resemble the holotype collection in most respects, but have 1- or 2-flowered spikelets in the same inflorescence, while yet others appear to be strictly 1-flowered. The last mentioned agree in this respect with some species of the genus *Calamagrostis (Deyeuxia).* The genus *Deschampsia* Beauv. is widely distributed in temperate and cold regions of both hemispheres, but occurs only at high altitudes in the tropics. Its spikelets are usually 2-, rarely 3- or 4-flowered, with the rhachilla continued beyond the uppermost floret as a fine, usually hairy bristle; its lemmas are 2-lobed, 4-toothed or lacerate at the apex, 4–7-nerved, awned from or above the base and with the awn geniculate or straight, and mostly with a bearded callus at the base of the floret. The specimens of *Mejland* 1556 are in many respects typical of *Deschampsia;* but although most spikelets are 2-flowered, in some the second floret has been found to be much reduced in size and moreover sterile, while 1- or 2-flowered spikelets occur in the same panicle. A similar condition has been noted in specimens of *Christophersen* 1105, the second floret being variously reduced, smaller and sterile, sometimes represented by only a minute hyaline rudiment or at times even without a vestige of the lemma, so that 1- or 2-flowered spikelets may be found in the same inflorescence. Much the same mixture has been observed in specimens of *Christophersen* 2469 from Inaccessible Island (plateau near west end, 450 m, 23/2/1938), although in this gathering 2-flowered spikelets appear to be of rare occurrence, while in those with 1 floret there is a minute rudiment of the second floret. Similarly, in specimens of *Mejland* 1383 from Tristan da Cunha (east of Hottentot Gulch, 600–700 m, 28/1/1938), 1-or 2-flowered spikelets occur in the same panicle but with the second floret imperfect and ranging from a microscopic vestige at the tip of the prolongation of the rhachilla to a minute lemma and no palea, or to a larger lemma and palea but with no flower, or sometimes with the vestige of a flower. These intermediate plants require investigation experimentally when plants become available for cultivation.

Deschampsia mejlandii C. E. Hubbard, **sp. nov.** (Fig. 28)

a *D. christophersenii* C. E. Hubbard, ligulis multo longioribus, foliorum laminis planis vel convolutis latioribus costis minute hispidis; lemmatibus paulo brevioribus minute scaberulis differt.

Densely tufted perennial, 12–48 cm high. Culms erect, relatively stout, stiff, simple, 1–2-noded, closely sheathed, glabrous, smooth. Leaf-sheaths persistent at the base, overlapping, coriaceous, glabrous, smooth, broad, up to 10 cm long; ligules lanceolate, 7–15 cm long, chartaceous-membranous, becoming lacerate; blades erect, stiff, linear, mostly pungent-acute, or subobtuse, with a hard involute coriaceous tip, 5–22 cm long, 2.5–6 mm wide, flat or convolute, glaucous-green or green, smooth beneath, prominently and closely ribbed above, with the ribs minutely hispid, scaberulous upwards on the margins. Panicles dense, erect or nodding, oblong or lanceolate-oblong, soft, silvery or very pale yellow (pallid), plumose, 10–25 cm long, 2–3.5 cm wide; rhachis mostly minutely hispid above; branches clustered, minutely hispid or rarely glabrous, up to 8 cm long, divided, closely spiculate; pedicels minutely hispid, 1–3.5 mm long. Spikelets oblong or gaping, 8–10 mm long, 2-flowered; rhachilla produced as a fine plumose bristle up to 1.5 mm long. Glumes narrowly lanceolate in profile, similar, equal or nearly so, firm below the middle, membranous above and at the margins, 3-nerved, with the lateral nerves below the middle; lower 6.5–8.5 mm long, narrowly oblong-lanceolate to narrowly elliptic-lanceolate opened out, acutely acuminate, keeled, scabrid above on the keel; upper up to 10 mm long, narrowly oblong-lanceolate opened out, acutely acuminate, keeled, scabrid above on the keel. Lower lemma 4–5 mm long, ovate to oblong-ovate opened out, unequally and acutely 4-toothed at the tip or 2-lobed with each lobe 2-toothed, thinly membranous, finely 5–7-nerved below the middle, minutely scaberulous, densely silky white villous on the basal callus with hairs

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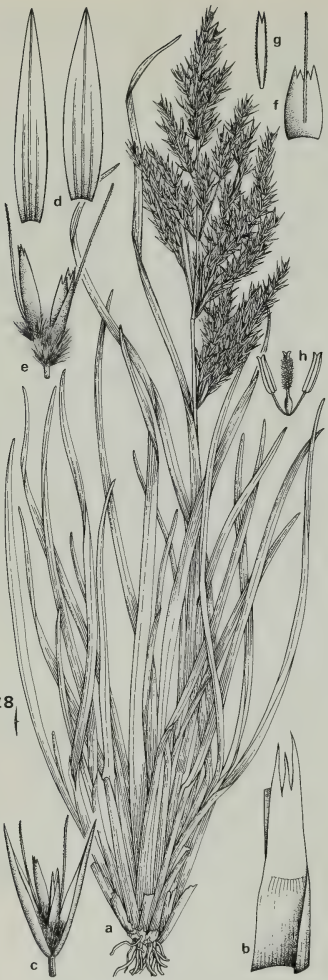

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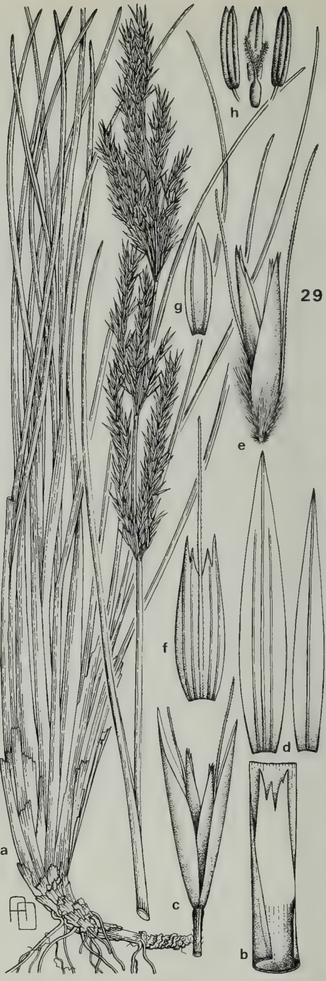

Fig. 28 *Deschampsia mejlandii* C. E. Hubbard. a. habit (x $\frac{1}{3}$); b. ligule (x $1\frac{1}{2}$); c. spikelet (x 3); d. glumes (x 4); e. floret (x 4); f. lemma (x 4); g. palea (x 4); h. stamens and ovary (x 5). All drawn from *Christophersen* 1106.

Fig. 29 *Deschampsia robusta* C. E. Hubbard. a. habit (x $\frac{1}{2}$); b. ligule (x 2); c. spikelet (x 4); d. glumes (x 5); e. floret (x 5); f. lemma (x 5); g. palea (x 5); h. stamens and ovary (x 10). The habit is a composite drawing based on *Wace* G. 245 and *Wace* G. 217; the ligule is drawn from *Wace* G. 217; the remainder are drawn from *Wace* G. 245.

2–3.5 mm long, awned; awn straight or slightly bent, 6–6.5 mm long, scaberulous, arising towards the base of the lemma; palea shorter than the lemma, narrowly oblong, acutely 2-toothed, 3–4 mm long, 2-keeled, minutely ciliate on the keels, thinly membranous; anthers 1–1.5 mm long. Upper lemma 3–4.5 mm long, ovate opened out, 2-lobed with the lobes unequally and acutely 4-toothed, finely 5–7-nerved below, minutely scaberulous, membranous, awned; awn straight, 4–6.5 mm long, arising near base of lemma; palea narrowly oblong, acute, 2-toothed, 3–3.5 mm long, minutely ciliate on the 2 keels, thinly membranous; anthers 1 mm long.

This grass has been named in honour of Mr Ingvar Mejland, botanical assistant on the Norwegian Scientific Expedition, 1937–38.

Endemic. First found on both Tristan da Cunha and Inaccessible Island by Christophersen and Mejland early in 1938 during the Norwegian Scientific Expedition. It occurred at several localities on Tristan da Cunha either at the upper limit of, or just above, the tree-fern zone. On Inaccessible Island it occurs in a meadow on the plateau near the western end.

Tristan: *Christophersen* 531 (O, K), 533b (O, K), 549a (O, K), 826* (O, K), 1106 (O, K -holotype); *Mejland* 1363 (O, K); *Stableford* s.n. (K); *Wace* T.15 (BM), T.74 (BM), T.165 (K), T.170 (K), T.176 pro parte (K), T.220 (K), T.247 (K), T.346 (K). **Inaccessible:** *Christophersen* 2764 (O, K).

Two other *Deschampsia* gatherings were made by Wace on Tristan da Cunha in October 1955: T.14 (BM) and T.78 (BM), both found in *Rumex/Holcus* grassland above Nellie's Hump at 750–1100 m. The first (T.14) might be a depauperate form of *D. mejlandi,* but its leaves seem different, being very short and rolled; the second (T.78) has some of the stems rooting at the nodes. Regrettably these gatherings lack spikelets and therefore it is not possible to say if they represent a distinct species. Collection of further material of both grasses from this locality is therefore desirable.

Deschampsia robusta C. E. Hubbard, **sp. nov.** (Fig. 29)

a *D. mejlandii* C. E. Hubbard, culmis altioribus robustioribus 2–5-nodis, laminis plerumque longioribus junciformibus involutis, paniculis laxiusculis latioribus, ramis scabridis vel laevibis differt.

A densely caespitose perennial, 80–110 cm high, from a short rhizome. Culms stout, terete, up to 5 mm in diameter, simple, 2–5-noded, glabrous, smooth. Leaf-sheaths glabrous, smooth; basal sheaths persistent, coriaceous glossy, up to 12 cm or more long; ligules lanceolate to ovate, acute, 8–15 cm long, membranous; blades junciform, with an acute or obtuse coriaceous tip, 20–45 cm long, tightly involute or opening out and up to 7 m wide, rigid, closely and prominently ribbed above, with the ribs shortly hispid, glabrous and smooth beneath. Panicles oblong-lanceolate to ovate, 15–25 cm long, 4–5 cm wide, inclined, somewhat loose: rhachis smooth in lower part, sparsely scabrid above or throughout; branches clustered, up to 10 cm long, scabrid or smooth; pedicels 1–6 mm long. Spikelets oblong or slightly gaping, 8–11 mm long, 2-flowered; rhachilla plumose, produced as a bristle beyond the second floret. Glumes as long as the spikelet, equal or almost so, narrowly lanceolate in profile, finely acute, firmly membranous, keeled, lower 1-nerved; upper 3-nerved, slightly wider than the lower. Lower lemma ovate-oblong when opened out, 2-lobed, with the lobes unequally and finely 2-toothed, chartaceous-membranous, 7-nerved, awned from one-fourth above the base; callus densely bearded with creamy hairs up to 3 mm long; awn 7.5–8.5 mm long, slightly bent, scaberulous; palea oblong, nearly as long as the lemma, 2-lobed, with the lobes acute, 2-keeled, with the keels ciliate, membranous; anthers up to 1.7 mm long. Upper lemma ovate-oblong when opened out, 4.5–5 mm long, 2-lobed, with the lobes unequally and acutely 2-toothed, membranous, 5-nerved, awned from the lowest third; callus densely bearded with hairs 2–3 mm long; awn up to 5 mm long, straight, scaberulous; palea narrowly oblong, nearly as long as the lemma, 2-keeled, with the keels ciliolate; anthers 1.5 mm long.

Endemic. First discovered on Gough Island by Wace in 1968. He found it growing at four separate localities, all in wet heath communities beside streams or in wet gullies. It is distinguished from the other Tristan da Cunha island group species by its taller, stouter, 2–5-noded culms.

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* Material collected under Christophersen 826 is much smaller than the other numbered gatherings but agrees in other respects.

Gough: *Wace* G.217 (K), G.223 (K), G.245 (K -holotype, BM), G.246 (K).

Deschampsia wacei C. E. Hubbard, **sp. nov.** (Fig. 30)

a *D. mejlandii* C. E. Hubbard, ligules brevioribus, laminis plerumque brevioribus angustioribus junciformibus involutis supra glabris, paniculis angustioribus, ramis laevibus differt.

A densely caespitose perennial, 6–40 cm high, with numerous leafy innovations. Culms erect, slender, 1–2-noded in the lowest fourth, simple, smooth. Basal leaf-sheaths persistent, coriaceous, glossy, 1–4 cm long, glabrous and smooth like the upper; ligules oblong- or ovate-lanceolate, acute, 2–10 mm long, membranous; blades juncaceous, rigid, curbed, 1–12 cm long, 0.6–1.3 mm in diameter, involute, closely and prominently ribbed above, glabrous and smooth. Panicles lanceolate to oblong, erect or inclined, contracted, 2.5–15 cm long, 1–1.5 cm wide; rhachis glabrous, smooth; branches unequal, up to 3 cm long, smooth-pedicels 1–4 mm long, smooth. Spikelets oblong or gaping, 9–10 mm long, 2-flowered; rhachilla produced as a fine plumose bristle. Glumes narrowly oblong-lanceolate in profile, oblong opened out, acute to slightly obtuse, equal or nearly so, as long as the spikelet, keeled, 1–3-nerved, glabrous, smooth, membranous. Lower lemma oblong-ovate when opened out, 5–6 mm long, 2-lobed, with the lobes very unequally and acutely 2-toothed and the teeth mucronate, membranous, finely 7-nerved, awned, smooth except for the minutely scaberulous apex; callus bearded with white hairs 1–2 mm long; awn arising on the back of the lemma in the lowest third, up to 10 mm long, straight or nearly so, minutely scaberulous; palea nearly as long as the lemma, lanceolate-oblong, 2-toothed, 2-keeled, scaberulous on the keels, thinly membranous; anthers 1.2–1.4 mm long. Upper lemma oblong-ovate when opened out, 4–5 mm long, 2-lobed, with the lobes unequally and acutely 2-toothed, membranous, 7-nerved, awned; callus bearded with white hairs up to 1 mm long; awn arising in the lowest third of the lemma, 8–9 mm long, straight or slightly bent, minutely scaberulous; palea oblong, 3 mm long, 2-keeled, with the keels minutely scaberulous, membranous; anthers 0.7 mm long.

This grass has been named in honour of Dr Nigel M. Wace, botanist on the 1955 Gough Island Scientific Survey Expedition.

Endemic. First found on Gough Island by Wace during his visit there in December 1955, thereafter in January 1956 and again in 1968. It grows at four separate localities, in bryophyte associations on wet peat or beside streams between 500-620 m. This species is characterised by its habit of forming small dense tufts of leafy innovations.

Gough: *Wace* (BM -holotype), 84, (BM), 118 (BM), G.218 (K), G.245 (K), G.302 (K).

Digitaria sanguinalis (L.) Scop.

Introduced. First collected on Tristan da Cunha near the Settlement by Stableford during 1953–54. It was found again in the same locality by Dickson in 1962, and by Wace in March 1968. A second locality for the species was discovered at the Potato Patches on Settlement Plain by Wace in March 1968. It is almost certain to have been introduced with imported fodder.

Tristan: *Dickson* s.n. (BM, K); *Stableford* 7a (K), 7b (K), 46 (BM); *Wace* T.128 (K), T.161 (K).

Echinochloa crus-galli var. **breviseta** (Doell) Neilr.

Introduced. Collected by Stableford during 1953–54. Possibly introduced with imported fodder, along with *Digitaria sanguinalis.*

Tristan: *Stableford* 3 (K), 45 (BM).

Eleusine indica subsp. **africana** (O'Byrne) Phillips

Eleusine africana O'Byrne

Introduced. Collected on Tristan da Cunha in February 1962, growing on bare ground at the Settlement.

Tristan: *Dickson* 122 (BM, K).

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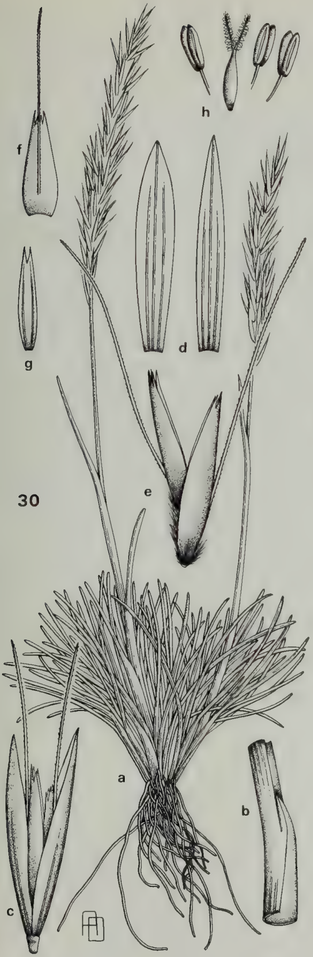

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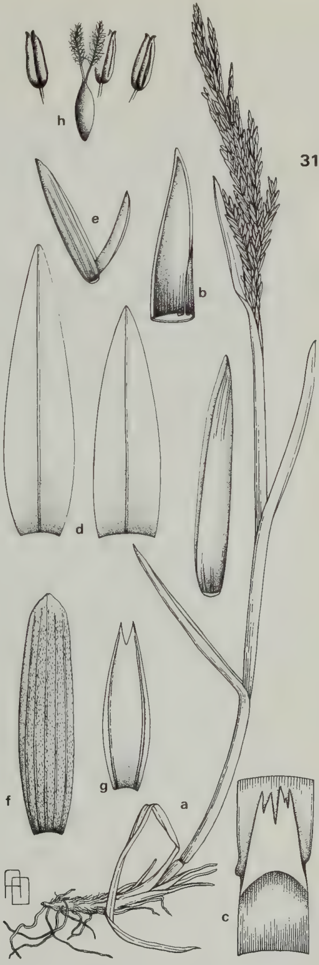

Fig. 30 *Deschampsia wacei* C. E. Hubbard. a. habit (x ⅔); b. ligule (x 4); c. spikelet (x 4); d. glumes (x 4); e. floret (x 5); f. lemma (x 4); g. palea (x 4); h. stamens and ovary (x 7). All drawn from *Wace* 21.

Fig. 31 *Glyceria insularis* C. E. Hubbard. a. habit (x ½); b. leaf tip (x 4); c. ligule (x 2); d. glumes (x 7); e. floret side view (x 7); f. floret opened side view (x 3); g. lemma (x 7); h. pales (x 7); i. ovary and stamens (x 8). All drawn from *Mejland* 1365.

Festuca arundinacea var. **mediterranea** Hackel ex Battend & Trabut

F. elatior subsp. *arundinacea* var. *geniuna* subvar. *mediteranea* Hackel

Introduced. Collected on Tristan da Cunha in December 1976, in the school enclosure at the Settlement. It was probably introduced with imported mixed American fescue pasture seed.

Tristan: *Wace* T.333 (K).

Festuca rubra subsp. **commutata** var. **barbata** (Hackel) Howarth

Introduced. First collected on Tristan da Cunha by Mejland in December 1937, being found in grassland by the Settlement. It was found again at the Settlement in 1962 by Dickson.

Tristan: *Mejland* 102a (O, K), 104 (O, K, BM); *Dickson* 123 (K).

Glyceria insularis C. E. Hubbard, **sp. nov.** (Fig. 31)

a *G. fluitanti* (L.) R.Br., foliorum laminis apice pungentibus cartilagineis, lemmatibus plerumque obtusis vel minute trilobis vel abrupte acutis; glumis longioribus, paleis lemmatibus multo brevioribus, antheris minoribus, differt.

Perennial, 25–55 cm high, rhizomatous, forming small tufts; shoots more or less compressed, 3–6 mm thick towards the base. Culms erect or ascending, closely sheathed, slender, simple. Leaves glabrous, green, sheaths, overlapping, smooth, striate and with scattered cross-nerves, the ribs obscurely vesiculate, ligules membranous, up to 10 mm long, becoming lacerate; blades linear, abruptly pungent-acute, with the tip cartilaginous, 6–21 cm long, 4–10 mm wide, folded, at length flat, smooth, ascending, firm with yellowish cartilaginous margins. Panicles linear to lanceolate, erect or slightly inclined, somewhat secund, dense, 0.5–1.5 cm wide, 12–24 cm long; rhachis slender, smooth, striate; branches erect, 2–3-nate, up to 5 cm long, 1–4-spiculate, smooth; pedicels 2–4 mm long, smooth. Spikelets linear-lanceolate to linear-oblong, 15–23 mm long, 2–3 mm wide, 6–10 flowered, green. Glumes acute or obtuse, membranous, 1-nerved, smooth; lower lanceolate to narrowly oblong-lanceolate, 3.5–7.5 mm long; upper oblong-lanceolate, 5.5–8 mm long, acute or obtuse. Lemmas* oblong-lanceolate to lanceolate-oblong, obtuse, apiculate, mostly minutely 3-lobed, rarely abruptly acute, 6–7.5 mm long, closely and minutely scaberulous, coriaceous except for the hyaline tip; 7-nerved. Paleas elliptic-oblong to oblanceolate-oblong or oblong, very shortly 2-toothed or entire, 4–5 mm long, with narrowly winged keels. Lodicules connate, truncate, very small. Anthers 1.3–1.8 mm long. Grain elliptic-oblong, dorsally compressed, 2 mm long, dark-brown, hard.

Endemic. It was first collected for the group in 1938, both on Tristan da Cunha and Inaccessible Island by Christophersen and Mejland during the visit of the Norwegian Scientific Expedition. The grass occurred mainly in damp grassy fields between 600–1000 m. It was found again on Tristan in 1968 by Wace by the crater-lake at Upper Cove, Gulch Hill, though nowhere abundant. Visiting Gough in 1956 Wace discovered it beside streams at two localities, i.e. in the crater of Edinburgh Peak and in the gullies of Gorydale. It was still present at these same sites when he was there in May 1968.

Tristan: *Christophersen* 1267 (O, K); *Mejland* 1365 (O, K -holotype), 1546 (O, K); *Wace* T.243 (K). **Inaccessible:** *Christophersen* 2347 (O, K), 2465 (O, K). **Gough:** *Wace* 135 (BM), 143 (BM), G.238 (K).

The two collections by Christophersen from Inaccessible Island cited above were at first considered sufficiently distinct to warrant description as a subspecies of *G. insularis;* but as this island has a large population of sea-birds, the greater vigour of the plants growing there is no doubt due to the highly nitrogenous nature of the soil. These two gatherings have taller culms 70–100 cm high, with thicker vegetative shoots 10–15 mm wide at the base; leaf-blades up to 40 cm long and 9–15 mm wide; ligules up to 16 mm long; panicles 24–36 cm long, 1.5–2 cm wide; branches many-spiculate, with the longer ones divided into short appressed branchlets. It is of interest to note here that on these two *Glyeria* numbers of Christophersen (2347 and 2465), the following fungi were identified by E. Müller of Zürich: *Anthostemella tumulosa* (Roberge) Sacc. (2465), *Ascochyta phleina* R. Sprauge (2347), *Gaeumannomyces graminis* (Sacc.) v. Arx & D. L. Olivier (2465), *Hendersonia culmicola* var. *minor* (Sacc.) Sacc. (2465), and *H. culmiseta* Sacc. (2465).

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* The only South American species of *Glyceria. G. multiflora* Steud., has shorter lemmas.

Holcus lanatus L.

Introduced. First collected on Tristan da Cunha by Bonomi in February 1904. Here it has now become very common throughout the island, and in 1955 Wace observed that it occurred in three main communities, viz. in grass heath above the Base, as a coloniser of bare soil and gravel, and in swampy ground, forming mats of vegetation over pools in gullies and deep turf in level, swampy areas.

Tristan: *Bonomi* 6 (NBG [herb. Mus. Austro-Afric. 1123], K), 7 (K, NBG [herb. Mus. Austro-Afric. 1123 bis]); *Christophersen* 5 (O), 289 (O, BM, K), 647 (O), 830 (O); *Dickson* 80 (BM, K); *Dyer* 3525 (PRE, NBG, BM), 3570 (PRE, NBG); *Keytel* 1833 (NBG, K, BM); *Mejland* 139 (O, BM, K); *Stableford* 14 (K), 35 (BM), 38 (BM), 85 (sterile) (BM); *Wace* T.28 (BM), T.255c (K). **Inaccessible:** *Christophersen* 2594 (O, K); *Wace* 1.2 (K). **Nightingale:** *Christophersen* 2098 (O, BM); *Wace* N.20 (K). **Gough:** *van der Merwe* 69 (PRE, K); *Wace* 52 (BM). 124 (BM).

Hordeum glaucum Steudel

Introduced. Found in 1953–54. Most probably it was introduced with animal fodder imported from Cape Town, South Africa, where it has been naturalised for many years.

Tristan: *Stableford* 1 (K), 43 (BM).

Hordeum leporinum Link

Introduced. Collected in 1968 beside the bull-pen in an old fenced garden west of Big Watron near the Settlement on Tristan da Cunha.

Tristan: *Wace* T.262 (K).

Lolium x **hybridum** Hausskn. SHORT-ROTATION RYE-GRASS

L. perenne x *multiflorum*

Introduced. First found by Stableford in 1953–54. Obviously an introduction in imported seed mixture.

Tristan: *Stableford* 9 (K); *Wace* T.158a (K).

Lolium multiflorum Lam.

Introduced. Found in 1953–54. Obviously an introduction with imported seed mixture.

Tristan: *Stableford* 42 (BM), s.n. (K).

Lolium perenne L.

Introduced. First collected by Mejland in 1937 on Tristan da Cunha, where it was growing in moist pasture at the Potato Patches. It was found again in 1962 by Dickson at the side of a track near the west end of the Settlement.

Tristan: *Dickson* 87 (BM); *Mejland* 160 (O, BM, K); *Stableford* s.n. (K).

Lolium rigidum Gaudin

Introduced. Found on Tristan da Cunha in 1968 by Wace who discovered it associated with other aliens (notably *Trifolium subterraneum*) in a levelled and seeded playing field north-east of the Settlement.

Tristan: *Wace* T.158 (K).

Parodiochloa C. E. Hubbard, **gen. nov.**

a *Poae* L. foliorum laminis tenuiter acutis, lemmatibus cuspidatis vel aristatis, stigmatibus elongatis breviter pulverulentibus differt.

Spikelets very numerous, oblong, becoming obcuneate, laterally compressed, cuspidate or awned, short-pedicelled on the branches of very dense panicles; rhachilla minutely and obscurely hairy or glabrous, disarticulating horizontally beneath each floret. Florets 2–4, ☿; rhachilla produced and bearing a vestigial floret; callus extremely short, truncate, glabrous. Glumes persistent, subequal or the lower slightly shorter, keeled, acute, herbaceous about the keel, otherwise hyaline-membranous, 1–3-nerved lower linear to narrowly oblong-lanceolate: upper narrowly lanceolate to narrowly oblong-lanceolate. Lemmas exceeding the glumes, contiguous, linear-lanceolate in side view, narrowly oblong or narrowly oblong-lanceolate when opened out, abruptly acutely acuminate, obtuse, truncate or slightly 2-lobed, 5-nerved, with the lateral nerves evanescent in the upper third and with the middle nerve passing into a prominent cusp or straight relatively stout scaberulous awn up to two-thirds the length of the lemma, thinly herbaceous except for the narrow membranous-hyaline margins and apex, minutely hispidulous or scaberulous. Paleas up to four-fifths the length of the lemmas, narrowly oblong, 2-keeled, concave between the minutely ciliolate or scaberulous keels, hyaline-membranous. Lodicules 2, oblong or obcuneate, 2-toothed or lobed, hyaline, glabrous. Stamens 3; anthers narrowly oblong. Ovary glabrous; styles 2, terminal, close together; stigmas elongated, very slender, minutely and loosely hairy, exserted from the apex of the floret. Caryopsis lanceolate, enclosed but free between the slightly hardened lemma and palea, keeled on the back, shallowly grooved or flattened adaxially, with a narrow membranous apical appendage; embryo about one-fourth the length of the caryopsis; hilum punctiform, basal. Perennial, forming large dense tussocks or clumps; culms erect, striate; leaf-sheaths compressed, keeled, closed (but splitting); ligules membranous, glabrous; blades elongated, folded in bud, at length linear and flat, long-attenuated to a fine point; panicles spike-like, continuous or lobed or interrupted. Monotypic.

Type species: *Parodiochloa flabellata* (Lam.) C. E. Hubbard.

The genus *Parodiochloa* may be distinguished from *Poa* by the finely pointed tips of the leaf-blades, the cuspidate or awned lemmas, and the elongated puberulent stigmas, which are exserted from the tip of the floret. Typical species of *Poa* possess hooded tips to the leaf-blades, obtuse to acute or acuminate, very rarely mucronate, tips to the lemmas, the latter usually being hairy on the nerves below the middle and often with a flake of woolly hairs at the base, and plumose bushy stigmas which are laterally exserted towards the base of the floret. *Poa cookii* is somewhat similar to *Parodiochloa* in its densely spike-like panicle, but, except for its mucronate-tipped lemmas, it has all the characteristics of a species of *Poa.*

Parodiochloa flabellata (Lam.) C. E. Hubbard, **comb. nov.**

Festuca flabellata Lam., *Encycl. Méth. Bot.* **2:** 462 (1788).—*Poa flabellata* (Lam.) Rasp. in *Ann. Sc. Observ.* **2:** 76, 78 (1829); J. D. Hook. in *Phil. Trans. R. Soc.* **168:** 22 (1879); Skottsb. in *K. svenska Vetensk Akad. Handl.* **50**(3): 14 (1913); Dallimore in *Kew Bull.* **1919:** 217 (1919); W. Davies, *Grasslands Falkland Is.:* **48** (1939).—*Dactylis caespitosa* G. Forster in *Commentat. Soc. Scient. gotting.* **9:** 22 (1789); Hook in *Lond. J. Bot.* **2:** 298, tab. 10(1843); J. D. Hook., *Fl. Antarct.* **2:** 384, tab. 136, 137 (1847).

Occurs in temperate South America, Falkland Islands, Fuegia (especially on treeless islands), South Georgia and Gough Island, and has also been introduced into the Shetland Islands (United Kingdom). It grows in the neighbourhood of the sea, on coastal cliffs and on mountain slopes. It is said to possess valuable feeding properties and is greedily eaten by grazing animals.

Introduced (?), As no collections of this grass seem to have been made on the group prior to this century, it is now thought unlikely to have ever occurred as native on Tristan da Cunha, Inaccessible and Nightingale Islands (Wace & Holdgate, 1976: 45). Had it been once as prominent on them as it is on Gough Island today, it seems unlikely that it would have been missed by the early visiting naturalists, particularly as the northern islands of the group were the more frequented by sailing vessels.

P. flabellata is now the dominant tussock grass on Gough Island, forming dense and pure communities on the western and northern cliff slopes, and also above the cliff tops on some of the more level ground below 300 m (Figs 20 and 32). It is also the principal dominant in some sheltered hollows at about 490 m to the south and west of Gonydale (Wace, 1961: 341–342). It is confined to areas of good drainage and the bottoms of hollows, although its distribution is in places clearly related to the extent of the penguin rookeries (Wace & Dickson, 1965: 307).

Gough: *van der Merwe* 30 (PRE, K); *Wace* 46 (BM), 87 (BM), G.207 (K).

Paspalum dilatatum Poiret

Introduced. First found on Tristan da Cunha by Dickson in February 1962 at the Settlement. It was collected there again by Wace in 1968, to the west of Big Watron amongst the New

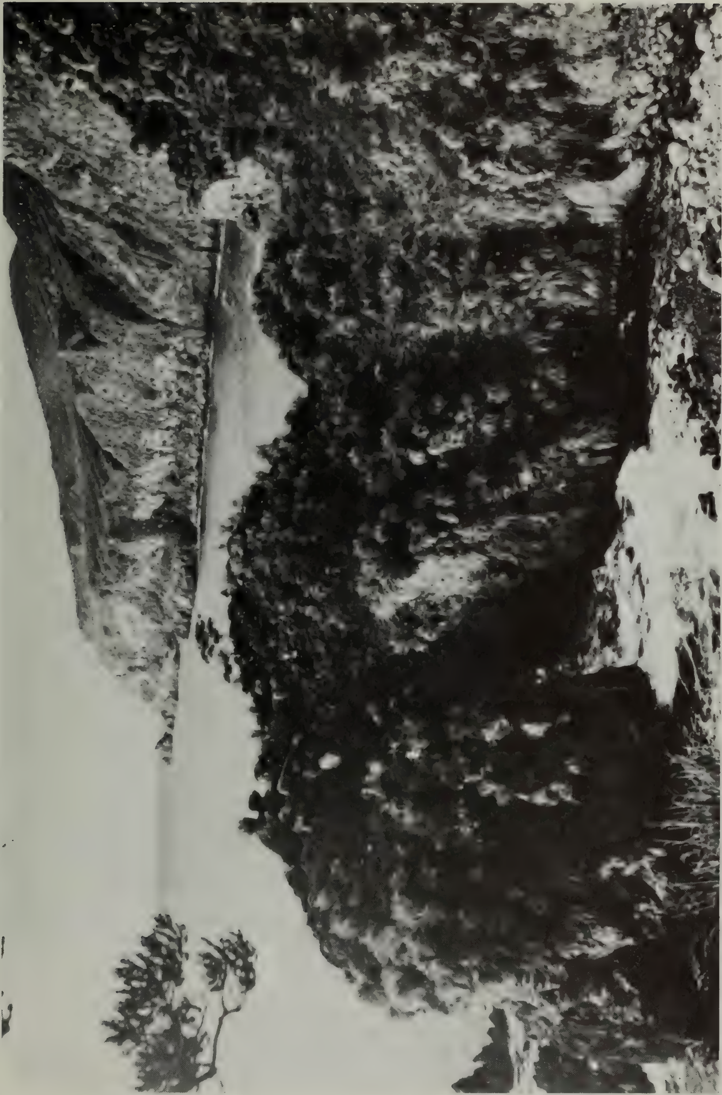

Fig. 32 Gough Island with Glen Beach and Archway Rock in the foreground, and Quest Bay and Haulround Point to the rear. Clumps of the grasses *Paradiochloa flabellata* and *Spartina arundinacea* clothe the Archway Rock and are surmounted by a few trees of *Phylica arborea*; fern bush, dominated by *Histiopteris incisa* var. *carmichaeliana*, covers the slopes of the cliffs above Quest Bay. May 1968. Photograph: Nigel Wace.

Zealand flax *(Phormium tenax)*, where it formed a thick growth in a sheltered situation, protected from grazing.

Tristan: *Dickson* 66 (K); *Wace* T.109 (K), T.180 (K), T.338 (K).

Pennisetum clandestinum Hochst. ex. Chiov.

Introduced. Collected on Tristan da Cunha in November 1976, where a clump was found colonising sand near the lagoon east of the new lava. Wace also noticed the species a month later forming conspicuous patches in newly sown pastures near the Settlement.

Tristan: *Wace* T.301 (K), T.321 (K).

Phalaris tuberosa L.

Introduced. Collected on Tristan da Cunha in February 1962 by Jenny's Watron on Settlement Plain.

Tristan: *Dickson* 81a (K).

Poa annua L.

Introduced. First collected on Tristan da Cunha by Macgillivray in 1852. Here it is frequent beside the lake in the Upper Crater by Cave Gulch, and has now also become a common weed at the Potato Patches and areas of disturbed ground below 1220 m. On Inaccessible Island it has been found about Blenden Hall, and on Nightingale Island along a trail path. On Gough Island it is frequent in wet peaty situations particularly near nests of the gony or Tristan subspecies of the wandering albatross *(Diomedea exulans dabbenena)* and around wallows of the elephant seal *(Mirounga leonina)* near to huts.

Tristan: *Christophersen* 9 (O, BM), 12 (O), 401 (O), 444 (O, K), 541 (O), 550K (O); *Dyer* 3530 (PRE, NBG, K); *Macgillivray* 344 (K); *Mejland* 133 (O); 1156 (O, BM, K); *Moseley* s.n. (BM, K); *Siggeson* 53 (O); *Stableford* 7a (K), 50 (BM); *Wace* T.50 (BM), T.245 (K), T.255b (K). **Inaccessible:** *Christophersen* 2384 (O), 2482 (O, BM, K); *Moseley* s.n. (BM, K). **Nightingale:** *Christophersen* 2157 (O); *Wace* N.61 (K). **Gough:** *Brown* s.n. (K); *Christensen* s.n. (O); *van der Merwe* 73 (K, PRE); *Wace* 44 (BM, G.201 (K), G.215 (K).

Poa infirma Kunth

Poa exilis (Tomm.) Murb.

Introduced. The presence of this species is based on a single gathering made on Tristan da Cunha by Mejland in January 1938 which was subsequently determined by Axel Nannfeldt. It was found growing at about 1000 m in the Hottentot Gulch. This widespread annual grass is a native from the Canary Islands, through the Mediterranean region and north Africa to north-west India. It has been introduced in other countries, including the British Isles, the Channel Isles, and South America.

Tristan: *Mejland* 1361 (O).

Poa pratensis L.

P. pratensis L. subsp. *pratensis*

Introduced. First collected on Tristan da Cunha by Moseley in 1873. It is a common grass there in more or less open communities at lower levels all over the island, especially in grassland near the Settlement and at the Potato Patches. Elsewhere it is often found colonising screes and loose soil in gullies. On Gough Island it is common around the huts and by the lower reaches of Glen Stream.

Tristan: *Christophersen* 63 (O, BM), 206 (O, BM, K), 294 (O), 539 (O, BM); *Dickson* 162 (BM); *Keytel* 1837 (NBG, K); *Mejland* 167a (O), 180 (O), 1356 (O, BM, K); *Moseley* s.n. (BM, K, E); *Wace* T.27 (BM), T.51 (BM). **Gough:** *Wace* 8 (BM).

Poa subcaerulea Sm.

P. pratensis subsp. *subcaerulea* (Sm.) Tutin

Introduced. This taxon is sometimes included as either a subspecies or variety of *Poa pratensis,* but Hubbard (1954: 169) considers it sufficiently distinct to be regarded as a separate species. The earliest collection was made on Tritan da Cunha in December 1937 by Mejland, who found it in pasture near the Settlement.

Tristan: *Dickson* 21 (BM, K), 88 (BM); *Dyer* 3625 (PRE, K), s.n. (K); *Mejland* 103 (O, K); *Stableford* 11 (K), 84 (BM), 89 (BM), 116 (BM); *Wace* T.349 (K).

Poa trivialis L.

Introduced. First found by Mejland on Tristan da Cunha in 1937 (determined by Nannfeldt and cited by Hafsten, 1951: 14), growing in pasture at the Settlement. It was found again at the Settlement in December 1976 by Wace, growing amongst New Zealand flax.

Tristan: *Mejland* 124 (O); *Wace* T.340 (K).

Polypogon mollis (Thouars) C. E. Hubbard & E. W. Groves, **comb. nov.,**

Pharlaris mollis Thouars, *Equisse Flore l'Isle de Tristan d'Acugna:* 37 (1808).—*Polypogon intermedius* Carmich. in *Trans. Linn. Soc. Lond.* **12:** 504 (1818).

A rhizomatous perennial, up to 75 cm high, rhizomes slender, spreading; culms relatively stout, clustered, geniculately ascending, simple, several-noded. Leaf-blades linear, up to 25 cm long and 8 mm wide, smooth or nearly so; ligules oblong, becoming lacerate, up to 6 mm long. Panicles continuous, or interrupted and ± lobed, very densely spiculate, 10–15 cm long, 1.5–2 cm wide; pedicels articulated at the base, 2–6 mm long, scabridly hispid. Spikelets continuous with and falling with the pedicels at maturity. Glumes stiffly and minutely hispid, equal or unequal, awned from the tips 5–7 mm long (including the awn), lanceolate, acutely acuminate, membranous, 1-nerved, the awn fine, scaberulous, up to 2.5 mm long, the upper glume shorter and slightly narrower. Lemma ovate, obtuse, 2–2.5 mm long, finely 5-nerved, with the lateral nerves minutely excurrent, aristulate and scabrid, the rest glabrous and smooth, awned from just below the tip, with the awn straight, 0.6–1.5 mm long; palea oblong, obtuse, 1 mm long, hyaline, nerveless; anthers 0.3–1 mm long; grain 1 mm long, elliptic-oblong, dorsally compressed.

Endemic. First collected for the group on Tristan da Cunha in 1793 by Aubert Du Petit-Thouars who published it (loc cit.) in his list under the name *Phalaris mollis.* A re-examination of this type material in Paris together with the original description shows that this grass belongs to the genus *Polypogon.* Carmichael, visiting Tristan da Cunha in 1816–17, found what he considered to be a new species of *Polypogon* which he published as *P. intermedius.* However, the type specimen is identical with that of Thouars' *Phalaris mollis.* The precise habitat details and localities are unknown for the only two specimens so far collected on Tristan, but the plants gathered on Inaccessible Island by Christophersen (February 1938) were found growing in a swampy depression near the western end of the plateau.

Tristan: *Carmichael* s.n. (BM -holotype of *P. intermedius*); *Thouars* s.n. (P -holotype of *P. mollis*). **Inaccessible:** *Christophersen* 2466 (O, K).

Polypogon monspeliensis (L.) Desf.

Introduced. Found on Tristan da Cunha by Keytel during 1908-09, and not found there again until 1968, when it was collected by Wace at the margins of freshwater swamps to the east and west of Pitbite, and also near the eastern edge of the new lava, growing amongst drifting beach sand and pebbles. It is a widespread grass in Europe, Africa and Asia and was introduced to Tristan da Cunha years ago, probably from South Africa.

Tristan: *Keytel* 1835 (NBG, K); *Wace* T.154 (K).

Spartina arundinacea (Thouars) Carmich. TUSSAC or TUSSOCK GRASS

Ponceletia arundinacea Thouars

Native. First collected on Tristan da Cunha by Aubert Du Petit-Thouars in 1793. This grass forms a tussock community on all of the islands, but on Tristan da Cunha its former native distribution along some of the coastal strips has been much reduced through clearing and firing and through the grazing of animals. Tussac was also cultivated along with flax on the inside of the walled cottage gardens, mainly to protect growing plants and vegetables from the strong winds (Christophersen, 1940: 26). From sea-level to about 100 m on that island it has been replaced by secondary grassland consisting of introduced species. In 1968 Wace found that on Inaccessible Island it was dominant both on the steep cliffs and on the more gently sloping ground burrowed by birds. On Nightingale Island in the same year he found that it was dominant over most of the island forming 'a bamboo-like dense cover with individual plants 2–2.5 m in height'. Earlier, in 1955, on Gough he found the tussocks to a height of 3 m and with a circumference of 1.5 m, growing along the shores and in clearings in the *Phylica* forest.

Tristan: *Christophersen* 288 (O, BM, K), 425 (O, K); *Carmichael* s.n. (BM); *Dickson* 1 (K), 30 (K), 99 (BM); *Dyer* 3576 (PRE, K), 3577 (PRE, NBG, K); *Macgillivray* 345 (K), s.n. (BM); *Mejland* 140 (O), 1170 (O), 1479 (O); *Milne* s.n. (K); *Moseley* s.n. (K, BM); *Siggeson* 56 (O); *Stableford* s.n. (K); *Swain* in Rogers s.n. (K); *Thouars* s.n. (P -holotype); *Wace* T.22 (BM). **Inaccessible:** *Christophersen* 2595 (O, BM, K); *Moseley* s.n. (K, E); *Wace* I.13 (K), I.14 (K). **Nightingale:** *Christophersen* 2167 (O, BM); *Stableford* 4 (K), 4a (K), 73 (BM); *Wace* N.13 (K). **Middle:** *Christophersen* 2020 (O, BM, K). **Gough:** *Brown* s.n. (K, E); *Christensen* s.n. (O); *Fleming* 36 (E); *van der Merwe* 60 (PRE, K); *Wace* 43 (BM).

Sporobolus africanus (Poiret) Robyns & Tournay HARD TWIT
S. capensis (Willd.) Kunth; *S. indicus* auct., non (L.) R.Br.

Introduced. First collected on Tristan da Cunha by Keytel, 1908–09. Since that date it has become abundant in pastures at the Settlement and on the lower slopes up to Burntwood.

Tristan: *Christophersen* 270 (O), 1322 (O); *Dickson* 3 (BM), 82 (K); *Dyer* 3541 (NBG, K), 3541a (NBG, K); *Keytel* 1836 (K); *Mejland* 1301 (O, BM, K), 1304 (O), 1305 (O), 1672 (O, BM, K); *Stableford* 5 (K), 47 (BM), 90 (BM); *Wace* T.88 (BM), T.110 (K), T.339 (K).

Vulpia bromoides (L.) Gray
Introduced. First collected on Tristan da Cunha by Macgillivray in November 1852. Christophersen (1937: 8) says of this widely distributed grass that 'it is probably of late introduction to Tristan da Cunha'. On Macgillivray's visit it was most likely to have been found at the Settlement, where, in the pastures, it has since been collected several times. It has also occurred at the Potato Patches, Seal Bay, Stony Beach and Hottentot Gulch. More recently, in 1968, Wace noticed it colonising the new volcano and growing on waste ground near the fish factory. It has also been found on Inaccessible Island where it was growing on talus above Blenden Hall.

Tristan: *Christophersen* 222 (O), 1132 (O), 1792 (O); *Dickson* 17 (K), 92 (BM), 166 (K); *Dyer* 3533 (NBG, K), 3533 bis (PRE); *Keytel* 1839 (NBG, K, BM); *Macgillivray* s.n. (K); *Mejland* 102 (O, BM), 109a (O); 113 (O, K), 1362 (O), 1418 (O), 1427 (O); *Milne* s.n. (K); *Moseley* s.n. (K); *Siggeson* 54 (O*); *Stableford* 1 (K), 1a (K), 1b (K), 33 (BM), 83 (BM), 87 (BM), 108 (BM); *Wace* T.120 pro parte (K), T.124 (K), T.126 (K), T.313 (K). **Inaccessible:** *Christophersen* 2485 (O).

[**Vulpia myuros** (L.) C. C. Gmelin
Festuca myurus L.
This species is listed by Christophersen (1937: 16) as being from Tristan da Cunha. He does not elaborate, but it is no doubt based on *Festuca myurus* given in the list of introduced plants observed by Moseley during the visit of HMS *Challenger* in October 1873 (Hemsley 1885: 145). C. E. Hubbard *(pers. comm.)* considers Moseley's voucher specimen, which is at K, to be *Vulpia bromoides* (q.v.).]

CONIFERAE

Pinus caribaea Morelet
Introduced. Wace & Dickson (1965: 333) mention the presence on Inaccessible Island of three trees situated behind the ruined cottage at Saltbeach. The trees appeared not to be regenerating when examined in 1968 (Wace & Holdgate 1976: 44–7). Wace & Holdgate (1976: 45) mention the existence of a pine plantation on Tristan da Cunha near Sandy Point but do not indicate the identity of the species.†

PTERIDOPHYTA

The arrangement for the families and genera follows Crabbe, Jermy, & Mickel (1975).

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* Not seen in Oslo herbarium in October 1973, but recorded as being there by Christophersen (1937: 8).

† An experimental introduction of some alien trees and shrubs to Tristan da Cunha, made in 1937, including *Pinus canariensis*, *P. halepensis*, *P. insignis*, and *P. pinaster* did not prove successful. Christophersen collected an herbarium specimen (No. 1785, now in O) of *P. radiata* on Tristan da Cunha in March 1938 from a tree in Gordon Glass's garden at the Settlement, obviously an introduction; it is not known if this tree survives.

LYCOPODIACEAE

Lycopodium diaphanum (Beauv.) Swartz DEVIL'S FINGERS

Lepidotis diaphana Beauv.; *Lycopodium clavatum* sensu Thouars, non L.

Endemic. First collected on Tristan da Cunha by Aubert Du Petit-Thouars in 1793. On Tristan it occurs mainly amongst fern scrub and in the *Phylica* forest up to 650 m, although it is locally common in the *Empetrum/Blechnum* heath at lower altitudes.

Tristan: *Carmichael* s.n. (BM); *Christophersen* 207 (O), 455 (O, BM, K), 529 (O), 1032 (O); *Dickson* 24 (BM), 151 (BM, AAS); *Dyer* 3563 (PRE, NBG); *Keytel* 1840 (NBG, BM); *Glass* s.n. (BM); *Keytel* s.n. [herb. Marloth 4701] (PRE); Herb. *Menzies* s.n. (BM); *Mejland* 1820 (O); *Richardson* s.n. (O); *Rogers* 1 (BM); *Stableford* 58 (BM); *Thouars* s.n. (P* -holotype of *Lepidotis diaphana*); *Wace* T.4 (BM), T.5 (BM). **Inaccessible:** *Christophersen* 2306 (O, BM, K); *Stableford* 123 (BM). **Gough:** *van der Merwe* 27 (PRE); *Wace* 101 (BM), 158 (BM).

Lycopodium magellanicum Swartz

Native. First collected on Tristan da Cunha by Christophersen in 1937, where it is common in wet peat in bogs and on mossy slopes in the *Phylica* forest. It has also been found on Gough Island, where it is frequent on blanket peat at about 300 m throughout the island.

Tristan: *Christophersen* 454 (O, BM, K), 1019 (O); *Dickson* 175 (BM); *Mejland* 1167 (O, BM); *Wace* T.1 (BM). **Gough:** *Wace* 19 (BM), 147 (BM).

Huperzia insularis (Carmich.) Rothm.

Lycopodium insulare Carmich.; *Urostachys insularis* (Carmich.) Herter; *Lycopodium saururus* Hemsley

Endemic. First collected on Tristan da Cunha by Carmichael in 1816. It is common on the islands in wet peat in bogs up to 760 m, sometimes forming clumps. A specimen collected by Christophersen on Inaccessible Island (No. 2356) and assigned by Christensen (1940: 23) to *L. selago* var. *hessei* Herter may possibly belong here.

Tristan: *Carmichael* s.n. (K -holotype of *L. insulare*); *Christophersen* 1021 (O, BM, K), 1066 (O), 1273 (O, BM, K); *Mejland* 1176 (O, BM); *Wace* T.2 (BM), T.3 (BM). **Inaccessible:** *Christophersen* 2356 (O, BM, K), 2475 (O); *Stableford* 122 (BM). **Nightingale:** *Christophersen* 2214 (O); *Crosbie* s.n. (E); *Moseley* s.n. (K, -holotype of *L. saururus*, E). **Gough:** *van der Merwe* 36 (PRE); *Wace* 20 (BM), 102 (BM), 159 (BM).

OPHIOGLOSSACEAE

Ophioglossum opacum Carmich.

Endemic. First collected on Tristan da Cunha by Carmichael, 1816–17, 'high on the dome' [presumably the Peak]. It has not been collected on Tristan since, but in 1956 it was found by Wace in three different localities on Gough Island, in wet peat amongst byrophytes, all above 600 m.

Tristan: *Carmichael* s.n. (BM -holotype). **Gough:** *Wace* 105 (BM), 146 (BM), 150 (BM).

ADIANTACEAE

ADIANTOIDEAE

Eriosorus cheilanthoides (Swartz) A. F. Tyron

Grammitis cheilanthoides Swartz; *Gymnogramma cheilanthoides* (Swartz) Kaulf.; *Asplenium filipendulaefolium* Thouars; *G. filipendulaefolia* (Thouars) Hook.

Native. First recorded on Tristan da Cunha by Aubert Du Petit-Thouars in January 1793, who published it as new under the name *Asplenium filipendulaefolium* in the text, but as *Grammitis cheilanthoides* in the caption to the plate (Aubert Du Petit-Thouars, 1808; 34 & tab. IV). It has since been found on that island on several occasions, and also on Inaccessible and Gough Islands, occurring on peaty rock ledges between 90–400 m. it exhibits considerable variation in size and leaf form, but clearly has a South American affinity (cf. Tyron, 1970: 129–133). Spores of this species were recovered by Hafsten from peat cores collected by N. M. Wace on Tristan da Cunha and Gough Island in 1955–56 (Hafsten, 1961). Tyron (1970: 61) commenting on his work considers that this fern has probably existed on the Tristan group for at least 5,000 years. The latter author is also of the opinion that Tristan examples of this fern 'are not distinguishable from some occurring in the Andes formerly called *E. elongatus* (Grev. & Hook.) Copel. or *E. flabellatus* (Grev. & Hook.) Copel.' (Tyron, 1966: 271).

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* Not seen on my visit in September 1975.

Tristan: *Carmichael* s.n. (BM, K, E [ex. herb. Menzies], E [ex. Wernerian Soc. volume]); *Christophersen* 202 (O), 210 (O, BM, K), 456 (O, BM); *Dickson* 158 (BM*); *Dyer* 3578 (PRE); *Keytel* 1847 (NBG); *Thouars* s.n. (P -holotype of *A. filipendulaefolium*, BM); *Wace* T.36 (BM). **Inaccessible:** *Christophersen* 2378 (O), 2502 (O), 2554 (O); *Stableford* 129 (BM). **Gough:** *van der Merwe* 17 (PRE), 21 (PRE); *Wace* 75 (BM), 104 (BM), 137 (BM).

Adiantum poiretii Wikstr.†

A. aethiopicum sensu Thouars, non. L.; *A. crenatum* Poiret (1826), non Willd. (1826)

Endemic. First found on Tristan da Cunha by Aubert Du Petit-Thouars in 1793 and recorded under the name *A. aethiopicum*. It occurs on the islands in gullies and crevices or under rock ledges in damp grass, sometimes where there is dripping water.

Tristan: *Bonomi* s.n. (NBG [herb. Mus. Austro-Afric. 1113]); *Carmichael* s.n. (BM, K); *Christophersen* 212 (O), 429 (O, K), 537 (O, BM); *Dickson* 20 (BM); *Dyer* 3560 (K); *Keytel* 1827 (NBG, K, BM); *Mejland* 181 (O); *Moseley* s.n. (K, BM); *Thouars* s.n. (P-in herb Jussieu -holotype of *A. crenatum and A. poiretii*, BM); *Wace* T.94 (BM). **Inaccessible:** *Christophersen* 2386 (O); *Moseley* s.n. (K). **Nightingale:** *Stableford* 7 (K). **Gough:** *Brown* s.n. (E); *van der Merwe* 53 (PRE), 75 (PRE); *Wace* 2 (BM).

VITTARIOIDEAE

Vittaria vittarioides (Thouars) C.Chr.

Pteris vittarioides Thouars; *Vittaria stricta* Carmich.

Endemic. First collected on Tristan da Cunha by Aubert Du Petit-Thouars in January 1793 and published as a new species. On Tristan it occurs mainly in the *Blechnum palmiforme/ Empetrum/Phylica* heath and in the *Phylica* forest, in which latter community it is also found on Gough Island. On Nightingale and Inaccessible Islands it has been found growing in gullies, in rock crevices and on rock ledges.

Tristan: *Carmichael* s.n. (BM -holotype of *V. stricta*, E [ex herb. Menzies]); *Christophersen* 527 (O, BM, K); *Dickson* 169 (BM); *Dyer* 3559 (PRE); *Mejland* 618 (O), 1625 (O, BM, K); *Thouars* s.n. (P -holotype of *P. vittarioides* [ex herb. Desvaux and ex herb. Bory de St. Vincent]); *Wace* T.33 (BM). **Inaccessible:** *Christophersen* 2377 (O); *Moseley* s.n. (K, P). **Nightingale:** *Christophersen* 2001 (O, BM, K), 2179 (O), 2226 (O, BM). **Gough:** *Brown* s.n. (K, E); *Wace* 54 (BM).

HYMENOPHYLLACEAE

Hymenophyllum aeruginosum (Poiret) Carmich.

Trichomanes aeruginosum Poiret

Endemic. First collected on Tristan da Cunha by Aubert Du Petit-Thouars in January 1793. This small fern, the largest specimens having fronds between 10–15 cm long, occurs frequently amongst moss, at the bases of other ferns and on trunks of tree ferns, often in dense shade. Occasionally it has been noted as growing on the faces of damp cliffs.

Tristan: *Carmichael* s.n. (K, BM, E); *Christophersen* 203 (O, BM), 245 (O, K), 452 (O, BM, K), 1245 (O), 1270 (O); *Dickson* 100 (BM); *Dyer* 3358 (PRE, NBG, K), s.n. (PRE); *Keytel* 1825 (NBG, K);

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* There is also an herbarium sheet in BM prepared from material cultivated at Leeds University of Dickson's original 1966 Tristan gathering.

† The name *A. poiretii* has, in the past, been applied to all forms of this taxon whether on the Tristan da Cunha islands or on continental Africa, with *A. thalictroides* as a synonym. Pichi-Sermolli (1957: 695), however, in a critical examination of numerous specimens, is of the opinion that the epithet *poiretii* should be reserved solely for the Tristan group taxon (where it is endemic) and that the continental African taxon (which has separate constant characters) should bear the epithet *thalictroides*.

Macgillivray 336 (K), s.n. (BM); *Milne* s.n. (K); *Moseley* s.n. (K, BM); *Thouars* s.n. (P -holotype*); *Wace* T.12 (BM). **Inaccessible:** *Christophersen* 2345 (O), 2614 (O). **Nightingale:** *Christophersen* 2034 (O, BM, K), 2211 (O). **Gough:** *van der Merwe* 74 (PRE); *Wace* 41 (BM), 64 (BM), 138 (BM).

Hymenophyllum peltatum (Poiret) Desv.†

Native. First collected on Tristan da Cunha by Siggeson in 1934 although possibly overlooked by earlier visitors. It is a frequent epiphyte on *Phylica arborea,* and is often found in association with the previous species on *Blechnum palmiforme* trunks. Fallen dead wood and peat banks in the *Phylica* scrub up to 500 m are also frequent habitats.

Tristan: *Christophersen* 58 (O), 78 (BM), 204 (O), 246 (O, BM), 678 (O), 827 (O, BM, K), 1057 (O, BM), 1225 (O); *Dickson* 102 (BM), 157 (BM); *Dyer* 3582 (PRE, NBG); *Mejland* 301 (O), 817 (O); *Siggeson* 36 (O). **Inaccessible:** *Christophersen* 2479 (O), 2496 (O). **Gough:** *van der Merwe* 20 (PRE); *Wace* 42 (BM), 65 (BM), 139 (BM).

Hymenophyllum tunbrigense (L.) Sm.

Native. Based on cytological work carried out on living ferns brought back by J. H. Dickson from Tristan da Cunha in 1966, Manton & Vida (1968) discovered amongst them *H. tunbrigense* (2n=26) on the island group, as distinct from the long established populations of *H. peltatum* (2n=36). Dickson's 1966 material had been found in Little Sandy Gulch on Tristan da Cunha, attached to the rhizomes of *Elaphoglossum laurifolium* growing on shaded vertical rocks at about 300 m. See also second footnote below.

Tristan: *Christophersen* 460 (O, BM, K), 1244 (O, BM); *Dyer* 3582 pro parte (PRE, NBG, BM); *Wace* T.11 (BM).

Trichomanes angustatum Carmich.

T. tenerum sensu Hemsley, non Sprengel

Native. First collected on Tristan da Cunha by Carmichael, 1816–17, who described his plant as a new species (Carmichael 1819: 513). On Tristan it occurs in *Blechnum palmiforme* scrub on rock and in shaded, damp places in gullies and ravines, and on Inaccessible Island on shaded, wet rocks, under *Spartina arundinacea.* Christensen (1940: 3) considers that this species is 'without any near African relative but exceedingly close to *T. tenerum* Spreng., a common species of tropical America (Mexico to south Brazil)'.

Tristan: *Carmichael* s.n. (K -holotype of *T. angustatum*); *Dickson* 32 (BM, AAS), 159 (BM, AAS); *Keytel* 1826 (NBG), s.n. (K); *Macgillivray* 335 (K); *Mejland* 191 (O, BM), 1149 (O, BM, K); *Milne* s.n. (K); *Wace* T.10 (BM). **Inaccessible:** *Christophersen* 2583 (O, BM, K); *Dickson* 142 (BM). **Nightingale:** *Stableford* 15 (K).

GRAMMITIDACEAE

Grammitis magellanica Desv. subsp. **magellanica**

Polypodium magellanicum (Desv.) Sturm.; *P. billardieri* var *magellanicum* (Desv.) C.Chr., *Grammitis billardieri* var. *magellanica* (Desv.) de la Sota

Native. First collected on Tristan by Carmichael in 1816, with further examples collected by Christophersen in 1937 and Wace in 1955. Wace also found it on Gough Island in 1956. It occurs in rock crevices and gullies and also on truncks of *Blechum palmiforme* and *Phylica arborea.*

Tristan: *Carmichael* s.n. (K-2 sheets); *Christophersen* 543 (O, BM), 1058 (O, BM); *Mejland* 1172 (O); *Wace* T.65 (BM). **Gough:** *Wace* 96 (BM), 148 (BM).

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* Poiret in his original description in Lamarck's *Encyclopédia Méthodique* **8:** 76 (1808) states that 'Cette plante a été recueillie par M. Borry de Saint-Vincent, dans l'Ile déserte de Tristan d'Acugna. (V.s. in herb du Petit-Thouars)'. Actually the reverse is true in that this specimen was collected from Tristan da Cunha by Aubert Du Petit-Thouars and then passed into Bory de Vicent's herbarium. from whence it later became incorporated in the collections at P.

† Christensen (1940: 56), in discussing the ferns collected during the Norwegian Scientific Expedition, 1937–38, on the Tristan da Cunha group recognised two varieties of *H. peltatum.* To the first of these, var. *menziesii* (Presl.) C. Chr. (based on *H. menziesii* Presl, known until then from southern Chile, Fuegia and Juan Fernandez), he assigned ten of the Christophersen and Mejland gatherings, and to the second variety, for which he proposed no name, he assigned *Christophersen* 460 and 1244 (both collected on Tristan da Cunha). Commenting upon the last two gatherings, Manton & Vida (1968: 366–7) considered that in the light of their cytological work on Tristan ferns 'there seems no doubt that they should in fact have been referred to *H. tunbrigense'.* These two gatherings have been cited in this present paper under *H. tunbrigense* (q.v).

Grammitis poeppigiana (Mett.) Pichi-Serm.

Polypodium poepiggianum Mett.; *G. australis* var. *nana* Franch.; *G. nana* (Franch.) Brack.; *G. billardieri* var. *magellanica* forma *nana* (Franch.) de la Sota; *Polypodium billardieri* var. *magellanicum* forma *nana* (Franch.) Skottsb.; *G. armstrongii* Tindale

Native. First recorded on Tristan by Christophersen in 1937 and later during the same expedition on Inaccessible Island and Nightingale Island. More recently (1956) it was collected on Gough by Wace, who noted that it was often depauperate. It occurs on the islands in similar habitats to *G. magellanica.*

Tristan: *Christophersen* 201 (O), 522 (O, K), 543 (O, BM), 631 (O, BM); 825 (O, BM, K); *Dickson* 120 (BM, AAS), 164 (BM); *Mejland* 172 (O), 1391 (O, BM). **Inaccessible:** *Christophersen* 2359 (O), 2589 (O). **Nightingale:** *Christophersen* 2032 (O -sterile), 2180 (O). **Gough:** *Wace* 112 (BM), 141 (BM).

Parris (in litt.) is of the opinion that *Christophersen* 201 'is an extremely large and most uncharacteristic *poeppigiana:* although the frond size is that of *magellanica,* as is the altitude, the spore size and habitat is of *poeppigiana.* Perhaps the specimen was collected from a very shaded and moist rock crevice.' Of *Wace* 141 she considers it to be 'an atypical *poeppigiana* because the habitat (above the forest line) is not of *magellanica,* which is almost always a forest epiphyte.'

DENNSTAEDTIACEAE

DENNSTAEDTIOIDEAE

Hypolepis rugosula var. **villoso-viscida** (Thouars) C.Chr.

Polypodium villoso-viscidum Thouars; *Cheilanthes viscosa* Carmich.

Endemic variety. First collected on Tristan da Cunha by Aubert Du Petit-Thouars in 1793 and described as *Polypodium villoso-viscidum.* On Tristan da Cunha and Inaccessible Island it grows amongst the *Blechnum palmiforme* scrub, and on Gough Island Wace noted it as occurring in the *Histiopteris* association. Christensen (1940: 7) says that the variety 'is very variable in size and shape . . .'.

Tristan: *Carmichael* s.n. (BM, K -holotype of *C. viscosa); Christophersen* 526 (O, BM); *Mejland* 1158 (O, BM, K); *Rogers* s.n. (K); *Thouars* s.n. (P -holotype of *P. villoso-viscidum).* **Inaccessible:** *Christophersen* 2498 (O, BM, K), 2503b (O), 2558 (O), 2621 (O). **Nightingale:** *Christophersen* 2178 (O), 2224 (O, K), 2233 (O, BM, K); *Dickson* 135 (BM); *Rogers* s.n. (K). **Gough:** *Wace* 30 (BM), 128 (BM).

Histiopteris incisa var. **carmichaeliana** (Agardh) C.Chr.

Pteris vespertilionis var. *carmichaeliana* Agardh

Endemic variety. First collected on Tristan da Cunha by Carmichael, 1816–17, the specimen being later decribed by Agardh (1839: 80) as a new variety in honour of the collector. On Tristan it occurs in the *Blechnum palmiforme/Empetrum/Phylica* heath, and on Gough Island it is common on the peat up to as far as the *Phylica* forest zone (Figs. 12 & 33).

Tristan: *Carmichael* s.n. (K -holotype BM); *Christophersen* 461 (O, BM, K), 528 (O, BM, K), 1063 (O); *Dickson* 176 (BM); *Fleming* 85 (E); *Keytel* 1840 (K), 1842 (NBG); *Macgillivray* 330 (K), s.n. (BM); *Milne* s.n. (K); *Rogers* s.n. (K); *Wace* T.41 (BM). **Inaccessible:** *Christophersen* 2555 (O); *Moseley* s.n. (BM, K, E). **Nightingale:** *Christophersen* 2004 (O, BM, K); *Moseley* s.n. (BM, K); *Rogers* s.n. (K); *Stableford* s.n. (K). **Gough:** *MacMillan* s.n. (PRE); *van der Merwe* 29 (PRE), 64 (PRE); *Swain* s.n. (L); *Wace* 11 (BM), 31 (BM).

THELYPTERIDACEAE

Amauropelta bergiana var. **tristanensis** Holttum

Dryopteris tometosa auct., non (Thouars) Kuntze; *Thelypteris tomentosa* auct., non (Thouars) Ching

Endemic variety. Aubert Du Petit-Thouars (1808: 32, 67), in his list of plants collected on Tristan on his way to the Mascarenes, published a new species *Polypodium tomentosum.* However, Holttum (1974: 134-5), after re-examining Aubert Du Petit-Thouars' type in the Paris herbarium, is of the opinion that the specimen was possibly wrongly localised, as the true *Polypodium tomentosum* (now *Amauropelta tomentosa* (Thouars) Holttum) is otherwise known only from Mauritius and Réunion.* Holttum (1974: 133-4) considers the Tristan-Gough taxon to be allied to *A. bergiana* (Schlectend.) Holtt., of mainland Africa, and has, therefore made it a variety, var. *tristanensis*. Carmichael's specimen, which would have been collected on Tristan da Cunha during 1816–17, is therefore the earliest authentic record. It occurs occasionally in the *Blechnum palmiforme/Phylica* scrub on Tristan da Cunha and Inaccessible Island, and in shaded places on Nightingale Island. On Gough Island Wace found it in thick *Phylica* forest, occasionally growing epiphytically near the ground.

Tristan: *Bonomi* 25 (NBG [herb. Mus. Austro-Afric. 1114], K); *Carmichael* s.n. (K -holotype of variety, BM); *Christophersen* 457 (O, BM, K), 644 (O), 1243 (O); *Dickson* 10 (BM), 153 (BM); *Keytel* 1829 (K), 1830 (K); *Mejland* 614 (O, BM, K); *Moseley* s.n. (K); *Wace* T.39 (BM). **Inaccessible:** *Christophersen* 2328 (O, BM), 2380 (O), 2526 (O, K), 2557 (O); *Dickson* 125 (BM). **Nightingale:** *Christophersen* 2186 (O, BM), 2220b (O). **Gough:** *Wace* 140 (BM), 156 (BM).

ASPLENIACEAE

ASPLENIOIDEAE

Asplenium alvarezense R. N. R. Brown

Endemic. First collected on Gough Island by R. N. R. Brown in April 1904, and described the following year (Brown, 1905: 247). It was not found on Tristan da Cunha until 1937–38, when Christophersen and Mejland discovered it there at a number of localities, it obviously having been overlooked by all previous visitors. On Gough Island it is dominant in the ground flora beneath *Histiopteris incisa* var. *carmichaeliana* over large areas. It has also been found on Inaccessible Island.

Tristan: *Christophersen* 548 (O, BM, K), 1017 (O); *Mejland* 1389 (O, BM), 1390 (O, BM, K), 1550 (O, BM, K), 1563 (O, BM, K). **Inaccessible:** *Christophersen* 2342 (O). **Gough:** *Brown* s.n. (E -holotype); *Wace* 1 (BM), 39 (BM), 62 (BM).

Asplenium erectum Bory

A insulare Carmich.; *A. marinum* sensu Thouars, non L.

Native. First collected on Tristan by Aubert Du Petit-Thouars in January 1793. It has also been found on Inaccessible, Nightingale and Gough Islands, and occurs on wet cliffs, in moist gullies, and on damp shaded rocks. Although Christensen (1940: 13) found variation between examples from Tristan da Cunha, he was unable to discover any good character by which they could be distinguished from *A. erectum* of South Africa, although he did describe the examples with most deviation as a variety, var. *aequibasis* (see below).

Tristan: *Carmichael* s.n. (K, BM—both syntypes of *A. insulare*); *Mejland* 1406 (O); *Thouars* s.n. (P, BM). **Inaccessible:** *Christophersen* 2344 (O); 2389 (O, BM), 2478 (L), 2580 (O), 2584 (O, B, K); *Dickson* 133 (BM, AAS); *Moseley* s.n. (K). **Nightingale:** *Christophersen* 2216 (O), 2227 (O, K); *Dickson* 139 (BM); *Moseley* s.n. (K); *Stableford* 12 (K). **Gough:** *McKinnon* s.n. (K); *Wace* 56 (BM), 131 (BM), 157 (BM).

The following specimens are recognised by Christensen (1914: 14) as var. **aequibasis** C.Chr.

Tristan: *Mejland* 1140 (O, BM, K – all intermediate between this and the type variety). **Nightingale:** *Christophersen* 2181 (O -holotype).

Asplenium monanthes L.

Native. First collected on Tristan da Cunha by Moseley in 1873 and since found several times mostly amongst moss in gullies and rock crevices.

Tristan: *Carmichael* s.n. (BM, E [ex herb. Menzies]); *Christophersen* 233 (O, BM), 421 (O), 519 (O, BM, K), 550 (O), 1240 (O, BM, K); *Dickson* 110 (BM), 168 (BM); *Mejland* 823 (O), 1139 (O, BM, K), 1392 (O); *Moseley* s.n. (BM); *Wace* T.46.

Asplenium obtusatum var. **crassum** (Thouars) C.Chr.

A. crassum Thouars

Endemic variety. First found on Tristan da Cunha by Aubert Du Petit-Thouars in 1793 and described as *Asplenium crassum* (Aubert Du Petit-Thouars, 1808: 71). It was subsequently reduced by Christensen in Christophersen (1937: 12) to a variety of *A. obtusatum* G. Forster, the type variety of which is found in Australia and New Zealand. The var. *crassum* differs in having much more densely serrated pinnae, which are more distinctly unequal-sided at the base (i.e. truncate above and more or less excised below) and by its more numerous and larger, ovate-acuminate scales on the rachis and underside (see also Christensen, 1940: 12). On Tristan da Cunha the variety often occurs on bare rock or in shaded rock crevices, and on Gough Island it has been found in caves where they may be only a small amount of light.

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* Du Petit-Thouars arrived in Réunion in 1795, where he spent some time gathering vascular plants, so confusion may have arisen during, or subsequent to, the time when he came to sort and label his collections.

Tristan: *Carmichael* s.n. (BM, K, E [ex Wernerian volume]); *Christophersen* 424 (O, BM, K), 446 (O); *Dickson* 45a (BM); *Dyer* 3561 (K, NBG); *Keytel* 1791 (K, NBG), 1832 (K, NBG); *Mejland* 145 (O, BM, K), 1160 (O), 1307 (O, BM, K), 1676 (O); *Moseley* s.n. (BM, K, E); *Rogers* s.n. (K); *Siggeson* s.n. (O); *Thouars* s.n. (P -holotype); *Wace* T.21 (BM). **Inaccessible:** *Christophersen* 2520 (O, BM); *Moseley* s.n. (BM, K); **Nightingale:** *Christophersen* 2097 (O); *Dickson* 134 (BM), 137 (BM); *Glass* s.n. (BM); *Moseley* s.n. (BM, K); *Rogers* s.n. (K); *Stableford* 8 (K), 14 (K), s.n. (K). **Middle:** *Christophersen* 2022 (O, BM, K). **Stoltenhoff:** *Christophersen* 2152 (O, K). **Gough:** *Brown* s.n. (E); *Fleming* 20 (E), 29 (E), 38 (E); *MacKinnon* s.n. (K); *Swain* s.n. (K); *Wace* 9 (BM), 40 (BM).

Asplenium platybasis var. **subnudum** C.Chr.

Endemic variety. Only a single gathering has been made of this interesting fern in *Phylica* forests on Inaccessible Island in 1938. The type of the species is known only from St Helena.

Inaccessible: *Christophersen* 2501 (O -holotype, BM, K).

ATHYRIOIDEAE

Athyrium medium (Carmich.) Moore

Aspidium medium Carmich.; *Asplenium medium* (Carmich.) Hook.

Endemic. First collected on Tristan da Cunha by Carmichael, 1816–17. It grows on wet rock in gullies and cliffs and occasionally be streamsides.

Tristan: *Carmichael* s.n. (BM, K-holotype); *Christophersen* 515 (O, BM), 1269 (O); *Dickson* 177 (BM); *Mejland* 1370 (O, BM, K), 1553 (O). **Inaccessible:** *Christophersen* 2467 (O), 2468 (O, BM, K), 2503a (O), 2522 (O).

DRYOPTERIDOIDEAE

Polystichum mohrioides (Bory) Presl

Aspidium mohrioides Bory

Native. A. Gepp identified this fern among the cryptogams collected by G. Wilkins, naturalist to the Shackleton-Rowett Expedition, 1921–22, when the *Quest* visited the group on its homeward voyage. Wilkins had found it on both Tristan da Cunha (*vide* Gepp's list of determinations of the Shackleton-Rowett cryptogams in BM) and also on Gough Island (Wilkins, 1925: 70). It is a southern species occurring in South Georgia, Amsterdam Island, Marion Island, the Falkland Islands and in the Andes of South America. Modern confirmation of its presence on Tristan da Cunha group is desirable.

Tristan: *Wilkins* 38 (BM)*. **Gough:** *Wilkins* 51 pro parte (BM)*.

Ctenitis aquilina (Thouars) Pichi–Serm.

Polypodium aquilinum Thouars; *Nephrodium aquilinum* (Thouars) Hemsley; *Dryopteris aquilina* (Thouar) C. chr.

Endemic. First collected on Tristan da Cunha by Aubert Du Petit-Thouars in January 1793. On Tristan da Cunha it is a common understorey associate of the *Phylica arborea* forest, and on Inaccessible Island it occurs beneath the tree fern canopy. On Nightingale Island it has been found in the tussock grass community, and on Gough Island in sheltered gullies and beneath *Phylica arborea*.

Tristan: *Barkley* in HMS *Challenger* s.n. (BM); *Carmichael* s.n. (E[herb. E. H. Layard and ex.

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* When searching the herbarium folders at the BM in March 1979, I was unable to locate the original voucher specimens. As some of Wilkins specimens were only scraps it is possible that his material was not kept after identification.

Wernerian volume]), s.n. (BM); *Christophersen* 23 (O, BM), 423 (O, BM, K), 1061 (O), 1093 (O); *Dyer* 3554 (PRE, NBG, BM); *Fleming* 52 (E), 72 (E), 90 (E), s.n. (E); *Keytel* 1828 (NBG, BM); *Macgillivray* s.n. (BM); *Mejland* 1575 (O); *Moseley* s.n. (BM, E); *Thouars* s.n. (P -holotype); *Wace* T.42 (BM), T.44 (BM). **Inaccessible:** *Christophersen* 2545 (O); *Moseley* s.n. (BM). **Nightingale:** *Christophersen* 2003 (BM, K), 2217 (O), 2232 (O); *Fleming* 57 (E). **Gough:** *Fleming* 18 (E); *van der Merwe* 6 (PRE), 53 bis (PRE); *Wace* 12 (BM), 133 (BM); *Wilkins* 88 (BM), 89 (BM) and 90 (BM).

Dryopteris wallichiana (Sprengel) Hylander

Aspidium paleaceum Sw.; *A. parallelogramma* Kunze; *Dryopteris parallelogramma* (Kunze) Alston; *D. paleacea* (Sw.) Hand-Haz

Native. First collected by Wace in 1956 from boggy places away from shade but with some shelter. It has fronds up to 1.5 m in height. This species is pan-tropical and is related to the European *Dryopteris affinis* (Lowe) Fraser-Jenkins *(D. borreri* Newman ex von Tavel; *D. pseudomas* (Wollaston Holub & Pouzer), for which the name *paleacea* has sometimes been mistakenly used.

Gough: *MacKinnon* s.n. (K); *Wace* 68 (BM).

ELAPHOGLOSSOIDEAE

Elaphoglossum hybridum (Bory) Moore

Acrostichum ciliare Thouars: *A. hybridum* Bory

Native. First collected on Tristan da Cunha by Aubert Du Petit-Thouars in 1793 and published as *Acrostichum ciliare.* The Tristan-Gough taxon has since been equated by Christensen (1940: 20) with the typical form of *Elaphoglossum hybridum* from Réunion and south Brazil. On Tristan it grows sporadically on moss-covered rock or in gullies in the mixed *Phylica/Blechnum palmiforme* association.

Tristan: *Carmichael* s.n. (E [herb. Menzies and ex Wernerian volume]); s.n. (BM, K); *Christophersen* 5501 (O), 690 (O, BM, K); *Dickson* 23 (BM, AAS); *Mejland* 617 (O, BM, K), 812 (O), 813 (O), 1148 (O, BM), 1617 (O); *Thouars* s.n. (P -holotype of *A.ciliare*); *Wace* T.32 (BM). **Inaccessible:** *Christophersen* 2362 (O, BM, K). **Gough:** *Wace* 160 (BM).

Elaphoglossum insulare C.Chr.

Endemic. First collected at Hottentot Gulch on Tristan da Cunha by Mejland in January 1938. It was found again by Dickson in 1962 growing on moss-covered rock at the same locality.

Tristan: *Dickson* 167 (BM, AAS); *Mejland* 1386 (O, BM, K), 1618 (O -holotype, BM).

Elaphoglossum laurifolium (Thouars) Moore

Acrostichum laurifolium Thouars; *A. conforme* Carmich., non Swartz

Endemic. First collected on Tristan da Cunha by Aubert Du Petit-Thouars in 1793. On Gough Island Wace in 1955 found it to be abundant amongst the *Empetrum* and tree-fern scrub at 355 m, and generally common on steep banks at lower altitudes.

Tristan: *Carmichael* s.n. (K -holotype of *A. conforme,* E [herb. Menzies]); *Christophersen* 449 (O, BM, K); *Dickson* 9 (BM); *Dyer* 3557 (PRE, NBG); *Keytel* 1831 (NBG), 1846 (NBG); *Mejland* 342 (O), 615 (O, BM, K); *Thouars* s.n. (P -holotype of *A. laurifolium*); *Wace* T.35 (BM). **Inaccessible:** *Christophersen* 2548 (O), 2582 (O). **Nightingale:** *Christophersen* 2092 (O, BM, K), 2115 (O); *Crosbie* s.n. (E); *Stableford* 11 (K). **Gough:** *Brown* s.n. (K, E): *Fleming* 1 (E); *van der Merwe* 77 (PRE); *Wace* 37 (BM), 114 (BM).

Elaphoglossum obtusatum (Carmich.) C.Chr.

Acrostichum obtusatum Carmich.

Endemic. First collected on Tristan da Cunha in 1816–17 by Carmichael. It occurs on moss-covered rocks in gullies and under *Phylica arborea.*

Tristan: *Carmichael* s.n. (BM, K -holotype, E [ex herb. Menzies]); *Christophersen* 538 (O, BM); *Dickson* 184 (BM); *Mejland* 811 (O, K), 1152 (O, BM), 1168 (O, BM), 1616 (O, K). **Inaccessible:** *Christophersen* 2316b (O), 2590 (O).

Elaphoglossum succisaefolium (Thouars) Moore

Acrostichum succisaefolium Thouars

Endemic. First collected on Tristan da Cunha by Aubert Du Petit-Thouars in 1793. On

Tristan da Cunha it is common in the *Phylica/Empetrum* scrub, especially on steep banks in association with *Blechnum palmiforme* and *Blechnum penna-marina* at altitudes mostly between 30–300 m. On Inaccessible Island it grows amongst the tree ferns, and on Nightingale Island it has been found on ledges and cliffs. On Gough Island it occurs frequently on steep peaty banks and on decaying trunks of old tree fern. It is by far the commonest species of *Elaphoglossum* occurring on the islands.

Tristan: *Barkly* in HMS *Challenger* s.n. (BM); *Carmichael* s.n. (BM, K, E [ex Wernerian volume]); *Christophersen* 208 (O); *Dickson* 95 (BM); *Dyer* 3556 (PRE, NBG, K); *Keytel* 1843 (NBG, K), 1844 (NBG, K), s.n. (PRE [herb. Marloth 4702]); *Macgillivray* 328 (K), s.n. (BM); *Mejland* 156 (O, BM, K), 343 (O, BM, K), 616 (O), 821 (O), 1409 (O), 1635 (O); *Milne* s.n. (K); *Moseley* s.n. (K, BM); *Rogers* s.n. (K); *Thouars* s.n. (P -holotype, K); *Wace* T.3a (BM), T.31 (BM). **Inaccessible:** *Christophersen* 2307, (O), 2361a (O), 2556 (O, BM); *Moseley* s.n. (K). **Nightingale:** *Christophersen* 2000 (O, BM, K), 2042 (O, BM), 2091 (O, K): *Crosbie* s.n. (E); *Moseley* s.n. (K); *Stableford* s.n. (K). **Gough:** *van der Merwe* 19 (PRE); *Wace* 38 (BM), 59 (BM), 70 (BM), 115 (BM).

DAVALLIACEAE

DAVALLIOIDEAE

Rumohra adiantiformis (G. Forster) Ching

Polypodium adiantiforme G. Forster; *Polystichum adiantiforme* (G. Forster)J.Sm.; *Aspidium coriaceum* Sw.; *Polypodium calyptratum* Thouars

Native. First collected on Tristan da Cunha by Aubert Du Petit-Thouars in 1793 and published as a new species, *Polypodium calyptratum* (Aubert Du Petit-Thouars, 1808: 33). It has been found several times on the island since its first discovery, mostly on cliffs, and also on Inaccessible and Gough Islands. On the latter Wace found that in 1966 it was plentiful on dry peat banks particularly where drainage was good. Christensen (1940: 18) comments that the species exhibits much variation throughout its geographical range and that it is possible that the Tristan-Gough taxon, which is closely related to some forms from Argentina and South Africa, may deserve varietal rank.

Tristan: *Bonomi* s.n. (NBG [herb. Mus.Austro-Afric. 1112]); *Carmichael* s.n. (E [ex herb. E. H. Layard]); *Christophersen* 17 (O, BM, K); *Dickson* 147 (BM, AAS), 179 (BM); *Dyer 3562 (PRE, NBG);* Fleming 39 (E); *Glass* s.n. (BM); *Mejland* 153 (O), 1410 (O, BM, K); *Moseley* s.n. (BM, E); *Siggeson* s.n. (O); *Thouars* s.n. (P -holotype of *Polypodium calpytratum*). **Inaccessible:** *Christophersen* 2571 (O); *Moseley* s.n. (K, P). **Gough:** *Fleming* 11 (E), 23 (E); *van der Merwe* 52 (PRE); *Wace* 36 (BM), 90 (BM).

BLECHNACEAE

Blechnum australe L.

Native. First collected on Tristan da Cunha by Aubert Du Petit-Thouars in January 1793 and published in his list (Aubert Du Petit-Thouars, 1808: 33). It grows commonly in gullies and rock crevices and sometimes on cliffs beneath *Phylica* or on boulder scree.

Tristan: *Bonomi* 26 (NBG [herb. Mus. Austro-Afric. 1115]), K, 28 (PRE, E); *Carmichael* s.n. (K, E [ex herb. E. H. Layard and ex Wernerian volume]); *Christophersen* 428 (O, BM, K), 1242 (O, BM); *Crosbie* s.n. (E); *Dickson* 155 (BM, AAS); *Dyer* 3522 (PRE, K); *Dyer* (coll. by an islander) s.n. (PRE, NBG, K); *Keytel* 1823 (NBG, K), s.n. (PRE [herb. Marloth 4718]); *Macgillivray* 331 (K), 332 (K); *Mejland* 111 (O), 158 (O), 816 (O), 1164 (O, BM, K), 1306 (O, K); *Milne* s.n. (K); *Moseley* s.n. (K, E); *Rogers* s.n. (K); *Siggeson* s.n. (O); *Thouars* s.n. (P); *Wace* T.25 (BM). **Inaccessible:** *Christophersen* 2308 (O), 2577 (O), 2600 (O, BM); *Moseley* s.n. (K, E). **Gough:** *Wace* 94 (BM), 100 (BM).

Blechnum palmiforme (Thouars) C.Chr. TRISTAN TREE FERN

Pteris palmaeformis Thouars; *Lomaria robusta* Carmich. *L. boryana* sensu Hemsley, non Willd.

Endemic. First collected on Tristan da Cunha by Aubert Du Petit-Thouars in 1793. It is distinguished from the South African species *Blechnum tabulare* (Thunb.) Kuhn, with which it has by some authors been united, by having the pinnae narrowed towards the base of the frond (Christensen, 1940: 11). (See Figs 11, 12 & 33).

Tristan: *Carmichael* s.n. (BM -holotype of *L. robusta,* E), s.n. (E[ex Wernerian volume and ex Herb. Menzies]); *Christophersen* 45 (O, BM), 642 (O, BM, K); *Crosbie* s.n. (E); *Dickson* 154 (BM, AAS), 163

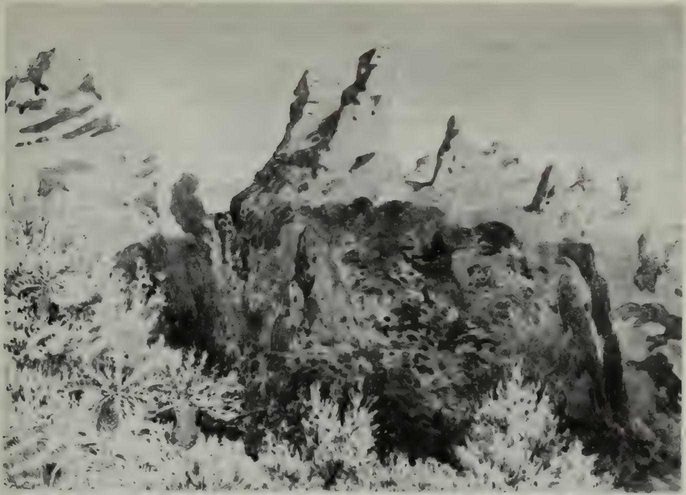

Fig. 33 Gough Island near the ridge peaks, with the ferns *Blechnum palmiforme* and *Histiopteris incisa* var. *carmichaeliana* and the island tree, *Phylica arborea,* forming the foreground. 8 June 1927. From an original watercolour by Sir Alister Hardy.

(BM), 174 (BM); *Dyer* 3555 (PRE, NBG); *Fleming* 78 (E); *Mejland* 157 (O); 1014 (O, K), 1437 (O), 1438 (O, BM), 1439 (O, BM), 1440 (O, BM, K), 1441 (O); *Thouars* s.n. (P -holotype of *P. palmaeformis*); *Wace* T.40 (BM). **Inaccessible:** *Christophersen* 2440 (O, BM), 2455 (O); 2559 (O); *Stableford* 121 (K). **Nightingale:** *Christophersen* 2212 (O, BM, K). **Gough:** *Brown* s.n. (E): *MacKinnon* s.n. (K); *van der Merwe* 40 (PRE); *Wace* 55 (BM), 67 (BM), 153 (BM), 154 (BM).

Blechnum penna-marina (Poiret) Kuhn

Acrostichum polytrichoides Thouars (text) [*'A. polypodioides'* below plate]; *Lomaria antarctica* Carmich.; *L. alpina* sensu Hemsley, non (R.Br.) Spreng.

Native. First collected on Tristan da Cunha by Aubert Du Petit-Thouars in January 1793. Here it has now become abundant on the steeper slopes, where it often forms a dense pure community; it also occurs up to 650 m in scrub associated with *Empetrum rubrum* and *Phylica arborea.* Examples cytologically investigated by Manton & Vida (1968: 372–3) were shown to differ from New Zealand plants of the same species that had long been under cultivation in Leeds University greenhouses. The Tristan material gave 2n=66; that from New Zealand 2n=68. In addition, the morphological differences between the Tristan and South American plants in comparison with those from Australasia indicate separation at subspecific level (A. C. Jermy, *pers. comm.*)

Tristan: *Bonomi* 26a (NBG), 28 (K); *Carmichael* s.n. (BM -holotype of *L. antarctic* s.n. (E [ex herb. Menzies]); *Christophersen* 4b (O), 209 (O), 471 (O), 1062 (O); *Dickson* 13 (BM); *Dyer* 3521 (PRE, K, NBG); *Fleming* 42 (E), 56 (E), 87 (E); *Glass* s.n. (BM); *Keytel* 1824 (NBG, K, BM). s.n. (PRE [herb Marloth 4718a]); *Macgillivray* 333 (K), s.n. (BM); *Mejland* 112 (O), 640 (O, BM, K); *Milne* s.n. (K); *Moseley* s.n. (BM); *Siggeson* s.n. (O, BM); *Stableford* 67 (BM), 81 (BM); *Thouars* s.n. (P -holotype of *A. polytrichoides,* BM); *Wace* T.24 (BM), T.34 (BM), T.66 (BM). **Inaccessible:** *Christophersen* 2553 (O). **Nightingale:** *Christophersen* 2037 (O); *Stableford* 13 (K), s.n. (K). **Gough:** *Brown* s.n. (K); *MacMillan* s.n. (PRE); *van der Merwe* 4 (PRE); *Wace* 13 (BM), 80 (BM), 106 (BM).

AZOLLACEAE

Azolla filiculoides Lam.

Native. Found only on Inaccessible Island, where two collections were made in 1938—one in a swamp at West Point, and the other in a brook on the beach at Blenden Hall. Dickson noted in 1962 that it was abundant on 'wet ground under *Spartina*, and especially on open water' at these two localities (Wace & Dickson 1965: 317 & photograph: Fig. 30). Christensen (1940: 23) considers that this widely distributed American species is probably of recent introduction.

Inaccessible: *Christophersen* 2446 (O), 2615 (O, BM, K).

Comments on the flora

Altogether 212 flowering plants and ferns are known from the islands of the Tristan da Cunha group. This figure comprises both native and introduced taxa at specific level or below. The native taxa are further divided into those considered *endemic* (i.e. not recorded outside of the islands) and those considered *native* in the strict sense (i.e. present on the islands for a very long time and with a wider distribution beyond the group):

Angiosperms	*Total taxa*
Endemic	34
Native (s.str.)	24
Introduced	119
Total	177

Pteridophytes	
Endemic	20
Native (s.str.)	15
Introduced	0
Total	35

A further breakdown of the above figures to show the totals for each island is as follows:

	Tristan	*Inaccessible*	*Nightingale*	*Gough*
Area (in sq. km)	86	12	4	57
Altitude (in m)	2060	*c.* 777	*c.* 300	910
Spermatophyte taxa				
Endemic	27	20	14	21
Native (s.str.)	20	17	7	15
Introduced	115	22	5	17
Pteridophyte taxa				
Endemic	19	17	12	15
Native (s.str.)	14	10	4	12
Total number of vascular plant taxa	195	86	42	80

As a result of critical study by Carl Christensen, A. H. G. Alston and A. F. Tyron, the pteridophytes are probably the most completely known and best understood taxonomically of all the major plant groups on the islands. Although it has been possible to correct hitherto uncertain names for some ferns it is some measure of the extent of the work that the number of taxa for this group of plants has only been increased by two since the 1965 list of Wace & Dickson. The two additions have come about as a result of generic revisions rather than by new discoveries in the field. Although it is probably unlikely that many new species of fern remain to be discovered on the islands, there is nevertheless much culture experimental work that still needs to be done on some of the species already known to occur in the Tristan da Cunha group.

It is not the purpose here to repeat the analytical and biological data on the flora given in Wace & Dickson (1965), and the reader is referred to that paper for the valuable information it contains. However, certain tables are presented here in a similar form so that a ready comparison may be made between the status of the flora then with that as it is known today. It has been possible during research for this present paper to examine all the hitherto unpublished collections of the Tristan-Gough vascular plants in the major herbaria which were not readily available to the authors just mentioned. It has also been possible to make taxonomic evalution on a number of species so as to bring their nomenclature in line with recent revisions.

Relationship of the flora of the Tristan da Cunha group of islands

By far the greatest number of native and endemic vascular plants of these islands have either a South American or a south circumpolar distribution, or are closely allied to species that have such a range. Although the islands are closer to southern Africa (see Fig. 2), the African element (i.e. related to species on that mainland) is with regard to the flowering plants quite small. Indeed, there is no native phanerogam present on the Tristan da Cunha group that is otherwise entirely confined to Africa. With the ferns, however, whilst 30 out of the islands' 35 taxa have close relatives in the southern part of South America, or are known from other Antarctic islands, the African connection in this group of plants is much stronger, with two-

Table 1 Spermatophytes of the Tristan da Cunha group of islands. Figures in brackets indicate the number of endemics.

	Whole Group	*Tristan*	*Inaccessible*	*Nightingale*	*Gough*
Native (s.lat.)					
Number of families	19	16	15	11	16
Number of genera	32	28	25	16	25
Number of taxa at species level or below	58 (34)	47 (27)	37 (20)	21 (14)	36 (21)
Number of taxa at species level or below recorded on one island only	18 (11)	9 (6)	2 (0)	1 (1)	6 (4)
Introduced					
Number of families	33	32	12	3	5
Number of genera	83	80	20	5	10
Number of taxa at species level or below	119	115	22	5	17
Total number of taxa at species level or below of both native (s.lat.) and introduced plants	177	162	59	26	53
Number of visits on which spermatophytes have been collected	23	17	7	7	8

Table 2 Pteridophytes of the Tristan da Cunha group of islands. Figures in brackets indicate the number of endemics.

	Whole Group	*Tristan*	*Inaccessible*	*Nightingale*	*Gough*
Native (s.lat.)					
Number of families	15	14	14	11	12
Number of genera	20	19	18	13	17
Number of taxa at species level or below	35 (20)	33 (19)	27 (17)	16 (12)	27 (15)
Number of taxa at species level or below recorded on one island only	7 (3)	4 (2)	2 (1)	0 (0)	1 (0)
Number of visits on which pteridophytes have been collected	22	15	4	7	8

Table 3 Native (s.str.) & endemic vascular plants known only from a single island in the Tristan da Cunha group. (N = native; E = endemic)

Species known only from Tristan da Cunha:

Nertera depressa forma *fimbriata* (E)
Calystegia soldanella (N)
Carex thouarsii var. *curvata* (E)
Scirpus chlorostachyus (N)
Scirpus verruculosus (N)
Agrostis crinum-ursi (E)
Agrostis holgateana (E)
Agrostis wacei (E)
Agrostis sp. *(Phalaris cespitosa)* (E)
Asplenium erectum var. *aequibasis* (E)
Asplenium monanthes (N)
Elaphoglossum insulare (E)
Hymenophyllum tunbrigense (N)

Species known only from Inaccessible Island:
Peperomia berteroana (N)
Calystegia tuguriorum (N)
Asplenium plastybasis var. *subnudum* (E)
Azolla filiculoides (N)

Species known only from Nightingale Island:
Cotula moseleyi (E)

Species known only from Gough Island:
Sophora microphylla (N)
Cotula goughensis (E)
Tetronicium magellanica (N)
Agrostis goughensis (E)
Deschampsia robusta (E)
Deschampsia wacei (E)
Dryopteris wallichiana (N)

(N.B. With more intensive collecting some of these species will undoubtedly be found on other islands of the group)

thirds of the taxa affiliated to that continent. Few of the pteridophytes have a range extending northwards beyond the equator into the northern hemisphere tropics, and only one, *Hymenophyllum tunbrigense*, has a distribution which includes areas within the north temperate zone.

Distribution of vascular plants within the islands

Tables 1-3 give a comparison of the numbers of families, genera and specific taxa occurring on each island for both flowering plants and ferns. Tristan da Cunha (the only inhabited island) has been visited and botanical collections made on it on a good number of occasions, but Inaccessible and Nightingale on the other hand, have received only few visits from botanical collectors.

Dispersal mechanisms of the native species

A detailed discussion on each of the three ways (by wind, sea and birds) by which the native terrestrial flowering plants could have arrived on the Tristan da Cunha islands has already been given by Wace & Dickson (1965: 301–309). Suffice it to mention here those authors' general conclusion that the evidence at present available suggests that external transport by birds of the plant diaspores (i.e. by hooked adhesion to feathers or down or by viscid adhesion to feet) 'has been the most important agency by which terrestrial plants have arrived on the islands; that sea flotation has been of some importance; and that air flotation has only been of importance in the dispersal of cryptogams'.

Spread of alien flowering plants

Whilst the relationship of the native species (s.lat.) of any remote oceanic island to the flora of adjacent land masses is always of importance, the arrival of alien species has become of

Table 4 Number of alien species found by the different plant collectors, arranged in chronological order of collection. The numbers in brackets give the progressive total at each date.

Date of visit	*Collector*	*Tristan*	*Inaccessible*	*Nightingale*	*Gough*
1793	Aubert Du Petit-Thouars	3	–	–	–
1816–17	Carmichael	2 (5)	–	–	–
1852	Macgillivray & Milne	10 (15)	–	–	–
1873	Moseley	3 (18)	5	–	–
prior to 1884	*vide* Hemsley	1 (19)	–	–	–
1904	Bonomi	12 (31)	–	–	–
1904	Brown	–	–	–	4
1908–09	Keytel	9 (40)	–	–	–
prior to 1910	referred to in Mrs Burrow's book	4 (44)	–	–	–
1922–25	Rev. and Mrs Rogers	1 (45)	–	–	–
1927	*Discovery* (W.S.) Expedition	–	–	–	1 (5)
1934	Siggeson	3 (48)	–	–	–
Feb–Mar 1937	Dyer	5 (53)	–	–	–
1937–38	Christophersen & Mejland	26 (79)	11 (16)	3	–
1953–54	Stableford	16 (95)	–	1 (4)	–
1955–56	Stableford	3 (98)	–	–	–
1955–57	Wace	2 (100)	–	–	7 (12)
1956–57	van der Merwe	–	–	–	4 (16)
1962	Dickson	6 (106)	4 (20)	–	–
1968	Wace	7 (113)	2 (22)	–	–
1972	Fleming	–	–	–	1 (17)
1976	Wace	2 (115)	–	1 (5)	–

increasing interest to biogeographers and students of plant dispersal. From the date of the first botanical investigation of the islands of the Tristan group in 1793 (when, along with native species, the earliest aliens *Chenopodium album, Lactuca scariola* and *Raphanus sativus,* were first noted) until 1899, 19 aliens had been found on Tristan and five on Inaccessible Island (see Table 4). From 1900 to 1929, 26 more were found on Tristan (making a total at the end of that period of 45), five on Inaccessible Island (no increase) and five on Gough Island. During the years 1930 to 1939 another 34 aliens were recorded on Tristan da Cunha (bringing the total to 79); 11 more on Inaccessible Island (bringing the total to 16); and three were found on Nightingale. No collecting was done on the islands during the decade 1940–1949, but from 1950 until 1968, due to more intensive and systematic collecting, the aliens for Tristan were increased by another 34, bringing the total there to 113; six more had been added from Inaccessible Island, bringing that island's total to 22; one more for Nightingale making four in all; and another 11 to those previously found on Gough, bringing the total to 16. The most recent aliens recorded were the two grasses *Festuca arundinacea* subsp. *mediterranea* and *Pennisetum clandestinum* found on Tristan in 1976 by Wace, bringing the total for that island to 115. *Phormium tenax* was noted on Nightingale bringing the total of aliens to five; and *Cerastium fontanum* subsp. *triviale* from Gough brings that islands total to 17. These numbers will undoubtedly be increased when all the material gathered during the 1968 and 1976 visits are distributed and become available for study (see p. 353). There have been no alien ferns recorded from the islands.

With perhaps the exception of *Chenopodium album, C. murale, Lactuca scariola, Raphanus sativus,* and *Rumex crispus* (all from Tristan da Cunha) the introductions are likely to be still present on the group. Most of these species seem to have originated from the Palaearctic region and to have arrived on the islands via the Cape Province of South Africa. Their numbers markedly increased during the period in which grazing animals, such as cattle, sheep and goats, were introduced. It will be of considerable interest to botanists to observe what further colonizers may be added to the alien flora of the Tristan da Cunha group of the islands in the years to come.

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* See Stafleu & Cowen (1976: 705) for publication details.

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